

**THE INFLUENCE OF GROWTH HABIT ON CARBON ASSIMILATION
AND DISTRIBUTION, LEAF CHARACTERISTICS AND YIELD IN
FIELD BEANS (VICIA FABA L)**

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THE INFLUENCE OF GROWTH HABIT ON CARBON
ASSIMILATION AND DISTRIBUTION, LEAF CHARACTERISTICS
AND YIELD IN FIELD BEANS (VICIA FABA L.)

By

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Title and subtitle The influence of growth habit on carbon assimilation and distribution, leaf characteristics and yield in field beans (<i>Vicia faba</i> L.).			
Abstract The growth habit of the field bean (<i>Vicia faba</i> L.) is indeterminate and this involves several problems. The continuous growth has a delaying effect on ripening and also makes the plant less threshable. In addition flower abortion and pod-set are negatively affected. Therefore this study was carried out to gather informations about the significance of the growth habit on carbon assimilation and plant development. The carbon assimilation and distribution patterns in indeterminate plants and a mutant with determinate growth habit as well as decapitated plants were studied by labelling whole plants with $^{14}\text{CO}_2$ at different stages of development followed by sequential harvestings at subsequent treatment dates. Furthermore an infra-red gas analyzer and a differential psychrometer were used for measuring net photosynthesis and transpiration rates during the ontogenesis of leaf 15 of indeterminate and decapitated plants and leaf 8 of the mutant. Changes in diffusion resistances, specific leaf weight, leaf proteins, chlorophylls and ribulose 1.5-biphosphate carboxylase were followed as well. The influence of decapitation and determinate growth on photosynthesis and yield components was also studied in field-grown field beans. Here the Shimshi method was used for photosynthesis measurements. The most photosynthetically active leaves were situated 5-6 nodes below the apex. As the plant grew this "center" moved upwards as lower leaves senesced. During this process photosynthesis decreased as a result of increased diffusion and transfer resistance through the stomata as well as into		A4 A5	
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the chloroplasts. The most limiting factor in the senescing leaf, however, judging by the high correlation found between proteins and photosynthesis, was the decreasing ribulose 1.5-biphosphate carboxylase activity. Decapitation caused an increase in the rate of photosynthesis which remained high for several weeks. Both the resistance through the stomata and mesophyll cells were decreased and the content of ribulose 1.5-biphosphate increased to a level where it is not likely to limit photosynthesis. The contents of soluble proteins, chlorophyll and mono- and disaccharides were increased as well. In indeterminate plants the leaves in the mid region, where all pods are situated, played the dominating role in supplying the pods with assimilates. Upper leaves, however, contributed with more than 30 % of the total plant assimilation. Their part increased as lower leaves senesced. Only 10 % of the ^{14}C fixed before pod-set was recovered in the seeds at maturity. During seed-filling up to 60 % of the initially fixed carbon was recovered in the seeds. Carbon fixed before pod-filling was lost in two phases. One rapid phase, where about 25 % of the ^{14}C was lost, and a second slower phase where 0.5-0.7 % was lost each day until maturity. Losses of ^{14}C fixed during later stages occurred principally in a rapid phase with an increasing rate from 1.2 to 3.2 %. In decapitated plants and the mutant the lack of upper leaves was partly compensated by increased photosynthesis of lower leaves. By decapitation pod-set was increased. In the field, contrary to the growth chamber, increased abortion of pods and seeds neutralized the positive effect on pod-set. Photosynthesis was also increased in decapitated field-grown plants, but this did not fully compensate the loss of upper leaves. It is suggested that the determinate plant can supply a high number of pods with assimilates. In the field, however, other factors than carbon assimilation seem to have determining influences on yield.

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THE INFLUENCE OF GROWTH MEDIA ON THE
ASSIMILATION AND DISTRIBUTION OF LEAF CHLOROPHYLLS
AND VITAMIN IN FIELD BEANS (*Vicia faba* L.)

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Abbreviations and symbols

ABA	=	abscisic acid
IAA	=	indole acetic acid
RuBPCase	=	ribulose 1.5-biphosphate carboxylase
P	=	rate of photosynthesis measured with the Shimshi methods
PN	=	rate of net photosynthesis (respiration excluded)
Pr	=	rate of photorespiration
Rs	=	rate of synthetic respiration
Rm	=	rate of maintenance respiration
PhAR	=	photosynthetically active radiation (380 - 740 nm)
ra	=	resistance of transfer across the boundary layer
rs	=	resistance to diffusive transfer through the stomata
rm	=	equivalent diffusive resistance to transfer in the mesophyll
rx	=	equivalent carboxylation resistance
Sink	=	An organ or plant part that receive assimilate or other metabolites.
Source	=	An organ or plant part that supply other parts of the plant with metabolites.

CHAPTER I

THE PROBLEM

1.1 The field bean and the indeterminate growth habit.

The field bean (*Vicia faba*), which originated in south-west Asia, has long been a cultivated plant. The cultivation started in the Mediterranean area in the early stone age and from there it spread all over the world. Today cultivation of field beans has an increasing economical value and several countries therefore have started large breeding programs. These efforts have been very fruitful especially in Great Britain and the DDR (Müntz et al. 1972). In Sweden the cultivation of field beans (about 4000 ha) is restricted to the southern parts. Even here the vegetative period is relatively long and variations in climate affect yield and yield stability.

The long vegetative period and the yield instability are related to the indeterminate growth habit that characterizes the field bean plant. Continuous growth of the top zone has a delaying effect on ripening and also makes the plant less threshable. In addition flower abortion and pod set are negatively affected. Field beans, as in many other pulse crops, produce an excess of flowers, of which 80-90% drop before reaching maturity (Kambal 1969). In such crops, decapitation has been practised (mainly in gardening) in order to increase pod set and growth. Factors like these have contributed to an increased interest in determinate lines of soybean (Hicks et al. 1969, Bernard 1972) and field bean (Sjödin 1971, Gehrig 1978).

1.2 A mutant with determinate growth habit.

In Svalöv a mutant with determinate growth was isolated from seeds of *Primus* which had been subject to two different treatments. Part of the material was treated with neutrons (35 rad) and the other with methyl methan sulphonate (0.015) (Sjödin 1971). The mutant Sv 0621 develops normally until the plant reaches the third or fourth inflorescence stage. At this stage further leaf development is inhibited and only a stipule and a single flower without peduncle develops at each of the next six to seven nodes and then it is terminated with a top flower. Unfortunately, the number of inflorescences is too low (3-4) to ensure sufficient yield capacity.

However, the character displays a recessive monofactorial inheritance and the expression of such a gene can be changed by changing the genetic environment (Gaul et al. 1968) which could lead to possible improvements. This is, however, time consuming, and thus it is important to study the effects of a changed growth habit on plant development and yield before too much efforts are laid down in breeding the mutant.

1.3 Outline of the present study.

Although the vegetative top growth may in many respects be disadvantageous, the fact that the indeterminate plant type has been favoured during the evolution process (Stebbins 1974), suggests that there must be some positive factors connected with the indeterminate growth habit. One of these could be the enlarged leaf area which, if carbon assimilation is a

limiting factor, has a positive effect. Carbon assimilation and utilization in indeterminate plants as well as in determinate plants was studied in the present investigation.

The study has mainly concentrated around two areas: (1) the significance of the top leaves as a source of assimilates and (2) the possibility for a plant to compensate for the loss of the top leaves.

In the study both normal plants (undecapitated and decapitated) and Sv 0621 were used. It was therefore also essential to study whether decapitation and genetic determination of a plant give rise to comparable effects on plant development and yield. If so, normal decapitated plants could be used in field trials to see how an improved "topless" mutant would yield. Furthermore, field experiments were performed to check whether the plant would react similarly under field conditions and under more controlled conditions in the growth chamber.

1.4 Literature review

1.4.1 Photosynthesis and its regulation.

Net photosynthesis (P_N) is limited by different types of resistance to diffusion and carboxylation of the CO_2 molecule (Gaastra 1959, Nobel 1974). On its way from the external air to the chloroplast the CO_2 molecule is subjected to several kinds of resistance to diffusion (Jarvis 1971). Firstly the layer of still air around the leaf makes up the so-called boundary layer resistance (r_a). This resistance is low ($0-1 \text{ s}\cdot\text{cm}^{-1}$) under field conditions and does not exert a limiting influence (Gaastra 1959). A far more important resistance is the stomatal resistance ($1-10 \text{ s}\cdot\text{m}^{-1}$) (r_s). A close association between rate of photosynthesis and stomatal opening has been reported in several studies (Gaastra 1959, Woodward and Rawson 1976, Ludlow and Wilson 1971). Especially during different stress conditions such as drought, heat and abnormal concentrations of CO_2 the stomata play a leading role in influencing the rate of photosynthesis (Gaastra 1959, Bierhuizen and Slatyer 1964b).

In unstressed plants the most limiting resistance is usually not at the stomata level but at the level where diffusion occurs through mesophyll cells and into the chloroplast. Together with a carboxylating resistance (r_x), the mesophyll resistance (r_m) in most studied species exhibits a dominating influence on photosynthesis (Ludlow and Wilson 1971, Woodward and Rawson 1976). Their separate contributions, however, are technically very difficult to determine. Chartier et al. (1970) and Ludlow and Wilson (1972) have reported that the carboxylating resistance (r_x) is 5-10 times lower than the mesophyll resistance (r_m). On the other hand, the close correlation found between photosynthesis and ribulose 1,5-biphosphate carboxylase (RuBPCase) activity suggests that carboxylating processes exert a limiting influence (Björkman 1968a,b, Wareing et al. 1968, Andreeva et al. 1971).

Not only r_s but also r_m and r_x are influenced by external factors such as drought (O'Toole et al. 1976), and light (Patterson et al. 1977), although internal factors play a dominating role.

Throughout the ontogenesis of a leaf, internal factors such as for example the contents of chlorophyll, proteins, and hormones are changed and thus affecting r_x . By these factors r_s is also changed through secondary effects on leaf thickness and chloroplasts (Ludlow and Wilson 1971, Gifford and Marshall 1973, Hodgkinson 1974, Fraser and Bidwell 1974, Woodward and Rawson 1976, and Andreeva et al. 1972).

Apart from environmental and ontogenetical influences, diffusion resistances and thus photosynthesis seem to be influenced by the demand for assimilate (Woolhouse 1974). During periods of low vegetative and reproductive growth, e.g. at anthesis of cereals, some varieties assimilate less CO_2 than during both early vegetative growth and seed-filling (see Evans et al. 1973).

In field peas the onset of flowering and subsequent fruit growth lead to a rapid doubling in photosynthesis of the whole plant (Lawrie and Wheeler 1974). Flinn (1974) also showed that leaflet photosynthesis in peas is regulated by the demand for assimilate from the subtended fruit during its development. He observed three well-defined peaks correlated with rapid elongation of the pod, inflation growth of the pod and rapid growth of the seeds.

While the occurrence of a sink regulation on the assimilation rate of a source organ is now firmly established there is less agreement as to how this control is exerted. Among the several hypotheses of sink regulated photosynthesis, the feed-back inhibition mechanism (see review by Neales and Incoll 1968) and the hormonal regulation mechanism (Sweet and Wareing 1968, Turner and Bidwell 1965) have been and still are intensively studied.

It is possible to influence leaf photosynthesis through manipulations of the sink or source activity. Hall and Milthorpe (1978) showed that removal of the rapidly growing fruit from *Capsicum* plant reduced the rate of net CO_2 uptake by its leaves by up to 30%. This reduction was associated with increases in both r_s and $r_m + r_x$. The concentration of soluble sugars in the source leaf was unaffected but that of the polysaccharides was changed. However, variations in $r_m + r_x$ were not closely related to these changes.

Thorne and Koller (1973) reported that by decreasing the source capacity of soybeans by shading all leaves but one, photosynthesis of this leaf increased. The RuBPCase activity was also increased significantly. The starch level was decreased 10-fold, while the sucrose level rose 3-fold indicating a negative effect of starch accumulation in the leaves on PN. r_s did not vary, but $r_m + r_x$ was significantly decreased.

Results like these favour the idea of a feed-back inhibition. Starch granules may cause increased physical resistance to CO_2 transfer across the mesophyll and through the chloroplasts to the grana. It has been shown that the effective pathlength of CO_2 transfer to the grana is affected by the presence or absence of starch granules in the chloroplast (see Thorne 1973). In other words r_m is affected. Biochemical and photochemical reactions also could be affected by starch granules (see Thorne 1973). Thus r_x (excitation resistance included) is also influenced. However, r_x could also be decreased by the increased RuBPCase activity. This does in fact point to an hormonal regulation by the sink acting on the protein synthesis or activation of RuBPCase (Thorne 1973).

Plant hormones such as auxins, gibberellins and cytokinins are known to affect the leaves with a concomitant effect on photosynthesis. Auxins (Turner and Bidwell 1965), gibberellins (Treharne et al. 1970), and cytokinins (Richmond and Lang 1957, Wareing et al. 1968, Threharne et al. 1970, Dyer and Osborne 1971, and Adedipe et al. 1971) all increases photosynthesis when sprayed on leaves. Other treatments which result in the cytokinin content being increased in the leaves, for example when cytokinin is applied to the roots (Thieman et al. 1974) or when the buds and laterals are removed (Meidner 1970, Gifford and Marshall 1973) have

similar influence upon the leaf. Just how plant hormones control photosynthesis has not been fully agreed upon. It is known for example that cytokinins influence stomatal opening (Wareing et al. 1968), protein and RNA synthesis (Fletcher 1969, Maass and Klämbt 1977), and chloroplast development (Fletcher et al. 1977). Auxins and gibberellins affect RNA and protein synthesis (Woolhouse 1974, Maass and Klämbt 1977, Threharne et al. 1970). ABA also affects stomata (Loveys and Kriedemann 1974).

1.4.2 Assimilation and distribution patterns.

Although the assimilation of carbon to some extent is regulated by the demand for photosynthate, the biological age of the leaf exerts a far more important influence on its rate of assimilation. In e.g. soybeans (see Shibles et al. 1975), and peas (see Pate 1975) maximum photosynthetic rate occur soon after a leaf is full-grown, photosynthetic capacity is then lost with increasing age of the leaf. Consequently, the assimilation follows a pattern determined by the ontogenetical status of the leaf (Ludlow and Wilson 1971, Gifford and Marshall 1972, Hodgkinson 1974, Fraser and Bidwell 1974, Woodward and Rawson 1976, Hall and Brady 1977, and Mondal et al. 1978). Therefore, the assimilation of carbon more or less follows an increase-maximum-decrease pattern from top leaves to the lower ones (Ludlow and Wilson 1971, Hodgkinson 1974 and Vačlavík 1975).

The assimilate distribution pattern is dominated by the distribution of growth. In soybeans, at the vegetative stage, the uppermost leaves export principally to the apex and young expanding leaves, the lower leaves export to the roots (Thaine et al. 1959). At the time of fruiting, export from a leaf is primarily to its own pods (Belikov 1955). In field beans Jaquiéry (1977) found by means of autoradiographies that the apex was a strong sink to all leaves during flowering. At the time of fruiting, however, only leaves near the apex supplied it with assimilates. These leaves also exported a major part of their assimilates to lower parts of the plant.

The regulation of the flow of assimilates is as important as the control and regulation of photosynthesis. As far as the regulation of photosynthesis is concerned not much is known about the mechanism behind the translocation processes. However, most workers seem to accept an active loading and unloading of the phloem. The transport mechanism in the phloem is a more controversial topic and until this is resolved the control and regulation of the flow of assimilates can only be a matter of speculation (Weatherly 1975).

1.4.3 Effects of defoliation and decapitation on the assimilation and distribution patterns and yield.

By excising either the leaves or apex it is possible to affect normal assimilation and distribution patterns (see rew. by Neales and Incoll 1968). In *Perilla* plants decapitation causes senescent leaves to start regreening. The leaves become thicker, nucleic-acid and protein content, as well as photosynthesis and respiration increase (Woolhouse 1967, Callow and Woolhouse 1973). Similar results have been reported for *Phaseolus vulgaris* (Wareing et al. 1968, Meidner 1970), *Medicago sativa* (Hodgkinson 1974) and *Lolium multiflorum* (Gifford and Marshall 1973). In *Phaseolus* and *Lolium* r_s changed after partial defoliation (Meidner 1970, Gifford and Marshall 1973). In *Medicago sativa*, however, it was $r_m + r_x$ that changed, whereas in *Phaseolus vulgaris* both r_s and $r_m + r_x$ changed.

In decapitated Pinto beans and pruned alfalfa shoots, photosynthetic CO_2 fixation increased 2-fold, total N increased up to 27-30% and endogenous cytokinin-like activity increased 8-fold (Pozsar 1978). The fact that cytokinin activity increased is interesting since kinetin sprayed on the leaves has the same effect as decapitation (Richmond and Lang 1957, Wareing et al. 1968, Treharne et al. 1970, Dyer and Osborne 1971, and Adedipe et al. 1971).

The distribution of assimilates is changed by defoliation and decapitation. In soybeans defoliation between the source leaf and the root increases the amount of assimilate translocated to the root (Thrower 1962), whereas more ^{14}C is recovered in the apex if defoliation is carried out between the source leaf and the apex (Thaine et al. 1959).

Other studies concern the effect of defoliation and decapitation on growth and yield. Pulse crops in particular, have been used in these experiments to study the interaction between vegetative and reproductive growth (McAlister and Krober 1958, Hicks and Pendleton 1969, and Egli et al. 1976a,b).

In soybeans defoliation during the pod-filling stage decreases yield by lowering seed number and seed size (Egli and Leggett 1976). Removal of terminal buds affects branching, height, and leaf area index; the total dry matter was decreased by 20%. However, seed yield was unaffected and the efficiency of seed production per plant weight was consequently increased (Bauer et al. 1976).

Lawn and Brun (1974) studied the effects of photosynthetic source-sink manipulations on symbiotic nitrogen fixation. They found that the fixation reached a maximum near the end of flowering and then declined. Increasing the photosynthetic source/sink ratio maintained nodule activity at a high rate, while decreasing the source/sink ratio reduced the nodule activity below the level of the control. They interpreted the results in terms of competition for photosynthates between pods and nodules.

By simulating growth Sinclair and de Wit (1976) showed that nitrogen supply directly limited the yield but that an increased carbon assimilation could increase yield through its effects on nitrogen assimilation. If on the other hand, photosynthesis was increased without a concomitant increase in nitrogen supply this actually would reduce yield. In such case, more nitrogen has to be re-translocated from vegetative parts to satisfy the greater demand from the pods. This accelerates senescence and the filling period is shortened.

Similar studies have also been done with field beans. In a comprehensive study Hodgson and Blackman (1957) analysed the effects of different densities and defoliations as well as shading treatments on plant development and yield. Decapitation increased the number of immature pods, but shading of the top leaves had the opposite effect. The number of mature pods, however, was lower in decapitated plants. Seed yield was decreased through a lower number of pods and smaller seeds. They concluded that competition for nitrogen and carbon assimilates, between vegetative and reproductive growth and between old and young pods was significant. Limited supplies of nutrients together with growth regulators seemed to regulate the yield.

McEwen (1972) and Tamaki et al. (1972) have studied the effects of partial defoliation. McEwen found that loss of leaves in the mid-zone of the plant had the greatest effect on seed yield and that no leaves were functioning at maximum photosynthetic efficiency. Tamaki et al. reported a serious reduction in yield when upper leaves were removed at the end of flowering

or at the green pod maturing stage. Early defoliation affected both pod set, number of seeds per pods, as well as seed size. Late defoliation affected only seed size. The starch content in the remaining leaves and the total sugar content in stems was lowered and as was the starch in seeds. However, nitrogen content was approximately the same as in the control plants. From this they concluded that the reduction of leaf area was responsible for flower, pod and seed abortion which resulted from insufficient supply of photosynthate.

Positive effects of decapitation have been reported by Kuznetsow and Bebin (1965). Topping carried out when the seeds at lower nodes begin to change colour (30-40 days before maturity) result in increased seed size and yield and the plants mature earlier. Decapitation has also been used at Svalöv, to increase pod set and hasten maturity of pods in greenhouse-grown field beans.

Root growth is also affected by different treatments. Townshend (see Leonard 1962) found that if lateral shoots were removed root growth increased, but as new shoots developed the growth rate of the roots was restored to the original level. Decapitation does also reduce root weight. Early decapitation reduces root weight more than does late (Gehringer 1978).

1.4.4 Studies of determinate plant types in other crops.

In soybeans there are cultivars with both indeterminate and determinate growth habits. Among determinate types there is also an intermediate type, which compared with both indeterminate and determinate lines, gives a greater yield (Hicks et al. 1969) or at least as compared with the indeterminate (Bernard 1972). Determinate lines give less yield (Hicks et al. 1969, Bernard 1972) and in addition the yield stability is also reduced (Thseng and Huang 1976).

In determinate types ^{14}C -assimilate is more mobile at the vegetative stage but less so at the reproductive stage as compared with indeterminate types (Yoshida and Gotoh 1975). This may indicate that the supply of retranslocated carbon assimilate in determinate plants is lower during those stages when the plant needs an optimum of assimilates. This could have a negative effect on the yield.

Egli and Leggett (1973) concluded that dry matter is accumulated more rapidly in determinate than in indeterminate types. Stephenson and Wilson (1978) also found that acropetal movement to racemes became increasingly important towards the apex of the determinate plant. However, they also concluded that the increase in dry weight of the uppermost racemes of a determinate type depended more on increasing both the rate of dry matter accumulation and the length of the accumulation period, than on achieving a greater redistribution of assimilate from lower leaves.

Similar studies on the vegetative and reproductive growth have been done on cotton (*Gossypium hirsutum* L.). The growth of the cotton plant is usually indeterminate but depending on environment and genetical background it can appear more like a determinate type (Eaton 1955, Quisenberry 1975).

In a study of the assimilate translocation and utilization Ashley (1972) showed that the primary source of photosynthate for a boll was its subtending leaf and that translocation between different parts was low. He therefore concluded that much of the top vegetative growth was ineffective and could have negative effects on the rate of photosynthesis of lower leaves through increased mutual shading.

Saleem and Buxton (1976) studied the soluble carbohydrate concentrations along the plant axis and found high concentration at the uppermost nodes and near the root. At fruiting nodes, however, it was low and they interpreted their results in agreement with Ashley's conclusions. Therefore the determinate type could be a better alternative than the indeterminate.

However, studies with determinate cultivars have shown that lint yield is lower, particularly under limited soil moisture conditions (Quisenberry and Roak 1976). This shows, as already stated by others (Leonard 1962, Ray et al. 1974), that determinate cultivars are more sensitive to drought, probably because of a smaller root system.

CHAPTER II

DETERMINATION OF ASSIMILATION AND TRANSLOCATION PATTERNS

2.1 Introduction

There are several studies of the patterns of assimilate distribution in both mono- and dicotyledonous plants (Stoy 1965, Wardlaw 1968, Hume and Criswell 1973, Pate and Flinn 1973). Among dicotyledons, studies with soybeans and peas are particularly relevant, since the growth of these has much in common with the growth of field beans.

Since the development of the technique with $^{14}\text{CO}_2$ our knowledge about assimilation and assimilate translocation has increased considerably. Thus labelling of individual leaves with $^{14}\text{CO}_2$ has revealed that assimilates are translocated to special sinks depending on age and position of the $^{14}\text{CO}_2$ -fed leaf and on the location of sites of active growth. During vegetative growth lower leaves translocate mainly to lower parts of the stem and to the roots. Younger leaves translocate to actively growing meristems in the apex. During reproductive growth, however, most assimilates are translocated to the nearest pods and seeds (Thaine et al. 1959).

Jacquiéry (1977) and Jacquiéry and Keller (1978, 1980) found that recovered ^{14}C , in seeds of field beans, after a translocation time of 24 h was less than 10% before end of flowering. However, during rapid pod growth this figure was 45%. Furthermore until end of the flowering period the apex imported assimilates from lower leaves. As the pod developed they took over as sinks of assimilates. At this time upper leaves also contributed with assimilates to the pods.

Even if the translocation of carbon assimilates normally follows a certain pattern, defoliation and genetical manipulations of the plant type have shown that there is elasticity in how the assimilates are translocated in the plant. Harvey (1974), when studying different leaf mutations in peas, found no marked effect on the distribution pattern of assimilates to the seeds between normal leaved plants and plants with only stipules and tendrils. Thus other parts of the plant can take over as a source for assimilates.

In the present study the assimilation and translocation patterns of ^{14}C -assimilates were studied in indeterminate varieties, as well as in the decapitated and mutant plants. A technique involving pulse labelling of plants with $^{14}\text{CO}_2$ at different stages of development followed by sequential harvests at subsequent treatment dates was used. This makes it possible to follow the dynamic pattern of assimilate movement in the plants.

2.2 Plant material

In the study, two commercial varieties of field beans with normal indeterminate growth, Primus (Svalöv) and Skladia (Breustedt), and the mutant Sv 0621 (Svalöv) with determinate growth were used.

The seeds were germinated on wet sand and planted in 1.5 litre clay pots containing medium heavy soil with one gram of the compound mineral fertiliser "Blåkorn". The pots were placed outdoors in a bed of sand and watered daily. Once every third week they were given a solution containing 5 g KH_2PO_4 and 5 g K_2SO_4 per litre.

2.3 Methods

2.3.1 Experimental design

Translocation experiments with ^{14}C were conducted in the summers of 1973 and 1975. In 1973 Primus and Skladia and in 1975 decapitated plants of Skladia and the "topless" mutant Sv 0621 were used. At two stages of development non-decapitated Skladia plants were also treated with $^{14}\text{CO}_2$ in 1975. Tables 2.1 and 2.2 show the stages of development at which treatment and harvest were performed consecutively. Three plants were harvested at each occasion.

2.3.2 Administration of $^{14}\text{CO}_2$

Uniform plants from the sand bed were selected, enclosed in a plexiglass assimilation chamber ($175 \times 50 \times 50 \text{ cm}^3$) and placed in a treatment cabinet with constant light intensity and temperature ($\text{PhAR } 31 \text{ Wm}^{-2}$ and 20°C). $^{14}\text{CO}_2$ was generated by adding lactic acid to a vessel containing a mixture of inactive Na_2CO_3 and $\text{Na}_2^{14}\text{CO}_3$. The air mixture was circulated through the assimilation chamber via a pump. Initial CO_2 concentration was calculated to 1500 ppm and the specific activity to $1.8 \mu\text{Ci mmol}^{-1}$ in 1973. In 1975 the activity was about 20% lower. This amount was enough for at least 10 min of assimilation without reducing the CO_2 concentration below the saturation point.

Prior to the exposure of $^{14}\text{CO}_2$ the plants were allowed to adapt to the experimental conditions by pre-treatment under the same conditions as those used during the exposure but with normal air instead of the radioactive air mixture. The pre-treatment lasted for 60 min. Thereafter the plants were fed with labelled CO_2 for 10 min. Then the lights were switched off and the system was emptied in darkness during a period of 45 min. One plant from each treatment was harvested immediately after opening the chamber and the remaining plants were placed outdoors, where they were raised until the time of harvesting (Tables 2.1 and 2.2).

2.3.3 Radiochemical analysis

At harvesting the plants were divided into leaves (leaflets, petioles and most of the stipules), stems, top zones, pods, seeds and roots. In 1973 the plants were also divided into three zones according to their growth habit. Zone A: lower 5-6 nodes, zone B: the middle nodes where all pods are situated, and zone C: the purely vegetative upper zone. In 1975 zone A and zone B were analysed together and in Sv 0621 the first two developed shoots were treated as one main shoot and the remaining branches as another fraction.

After harvesting the plant parts were dried to a constant weight at 80°C, weighed and ground through a 40 mesh screen in a Wiley mill. 30 mg of the sample was combusted in oxygen in a closed bottle. The CO₂ was absorbed in 10 ml scintillation liquid containing 6 g PPO, 200 mg POPOP, 120 ml ethanolamine, 400 ml ethylene glucolmonoethylether and 480 ml toluene per litre. The samples were counted in a Packard Tri-carb liquid scintillation spectrometer. The channel ratio method for quench correction was used. Disintegrations per minutes (dpm) per plant part and percentage of total initial ¹⁴C present in each plant part are presented in the results. Standard error of the mean ($\pm$ S.E.) was calculated.

Table 2.1 Stages of plant development during which Primus and Skladia were treated with ¹⁴CO₂.

Stage	Date of treatment	Plant development
I Initiation of flowering	6.6 ¹⁾	Mainly zone A was developed. Ca 7 expanded leaves. Some flower buds at the apex. ²⁾
II Early pod development	26.6	Zone A and most of zone B developed. Ca 15 expanded leaves, 7-8 inflorescences, rudimentary pods at lower flowering nodes.
III Late pod development	3.7	Zone A and zone B developed. Zone C developing. 19-20 expanded leaves, 8-9 inflorescences. Relatively well developed pods at the first 4 flowering nodes.
IV Early seed development	10.7	23-24 expanded leaves, 8-9 inflorescences. Developed pods with seeds at the first 4 flowering nodes.
V Rapid seed development	24.7	Senescent leaves at zone A, big seeds in most pods.
VI Late seed development	31.7	Most leaves senescent. Lower leaves abscised.
VII Maturity	14.8	Plants dry. All leaflets abscised.

¹⁾ Skladia was treated one day after Primus.

²⁾ For explanation of Zone A, B and C see 3.3.1.

Table 2.2 Stages of development during which decapitated Skladia and Sv 0621 plants were treated with $^{14}\text{CO}_2$.

Stage	Date of treatment	Plant development	
		Sv 0621	Decapitated Skladia
I Initiation of flowering	13.6 ¹⁾	9 expanded leaves, initiation of flowering.	10 expanded leaves, initiation of flowering.
II Early pod development	1.7	11 expanded leaves, 3-5 inflorescences, 1-2 lateral branches, rudimentary pods.	17 expanded leaves, 10 inflorescences. All plants decapitated at this stage even those treated 13.6. All lateral branches removed.
III Late pod development	8.7	Well developed pods on main shoots and smaller ones on the first lateral branches. Otherwise as for II.	Well developed pod at the first 4 flowering nodes. Lowest leaves senescent. No lateral branches.
IV Early seed development	15.7	The main shoot plus two large lateral branches and several smaller ones developed. Pods with seeds. Leaves still very green and vigorous.	Well developed pods at all but the uppermost nodes. Lower leaves senescent.
V Rapid seed development	29.7	Well loaded pods. Some plants showed initiation of senescence.	Well loaded pods. Lower leaves abscised.
VI Maturity	16.8	Plants dry, most of the leaves not abscised.	Plants dry, most of the leaflets abscised, only petioles left.

¹⁾ Skladia were treated two days after Sv 0621.

2.4 Results

2.4.1 Dry matter accumulation

Weather conditions in 1973 and 1975 for June, July and August were quite similar except for the mean air temperature in August which was 20% higher in 1975 and for the number of sunlight hours which was 10% lower in July 1975 (see Table 6.1).

Tables 2.3 and 2.4 show dry weights from initial flowering until maturity. Primus and Skladia showed similar growth patterns, apart from a somewhat higher vegetative top growth in Primus. Total dry matter accumulation in decapitated Skladia plants and Sv 0621 were also similar, in spite of the fact that Sv 0621 produced more than one shoot. Seed weights in Sv 0621 were lower, however, but since more vegetative material was produced, this did not have any effect on total dry weight.

Table 2.3 Dry matter (g) of field bean plant parts after various harvesting times during 1973. Mean $\pm$ S.E., n = 6-27.

PRIMUS

Harvest date	6.6	26.6	3.7	10.7	24.7	31.7	14.8
A leaves ²⁾	1.62	1.12 $\pm$ 0.07	1.10 $\pm$ 0.08	0.86 $\pm$ 0.05	0.79 $\pm$ 0.07	0.79 $\pm$ 0.07	-
B leaves	-	3.45 $\pm$ 0.08	3.69 $\pm$ 0.22	3.66 $\pm$ 0.22	3.39 $\pm$ 0.19	2.51 $\pm$ 0.19	-
A stem	1.31	3.82 $\pm$ 0.36	5.22 $\pm$ 0.35	5.28 $\pm$ 0.30	5.57 $\pm$ 0.24	4.68 $\pm$ 0.21	4.11 $\pm$ 0.12
B stem	-	1.65 $\pm$ 0.04	3.15 $\pm$ 0.29	4.28 $\pm$ 0.03	4.68 $\pm$ 0.27	4.36 $\pm$ 0.19	3.79 $\pm$ 0.14
Top	-	-	1.56 $\pm$ 0.08	2.76 $\pm$ 0.37	2.98 $\pm$ 0.12	2.65 $\pm$ 0.25	0.59 $\pm$ 0.04
Pods	-	0.66 $\pm$ 0.09	1.39 $\pm$ 0.12	3.47 $\pm$ 0.17	5.35 $\pm$ 0.42	5.24 $\pm$ 0.23	4.06 $\pm$ 0.20
Seeds	-	-	-	0.83 $\pm$ 0.13	6.05 $\pm$ 0.32	10.88 $\pm$ 0.70	13.59 $\pm$ 0.54
Root	1.00 ¹⁾	2.18 $\pm$ 0.18	3.04 $\pm$ 0.24	3.64 $\pm$ 0.20	4.49 $\pm$ 0.17	3.56 $\pm$ 0.13	3.33 $\pm$ 0.22
Total	3.93	12.88 $\pm$ 0.67	19.17 $\pm$ 0.68	24.78 $\pm$ 0.67	33.30 $\pm$ 0.80	34.67 $\pm$ 1.15	29.47 $\pm$ 0.95

SKLADIA

Harvest date	8.6	28.6	5.7	12.7	26.7	1.8	14.8
A leaves	1.64	1.14 $\pm$ 0.06	0.98 $\pm$ 0.10	0.93 $\pm$ 0.15	0.67 $\pm$ 0.08	0.62 $\pm$ 0.06	-
B leaves	-	3.11 $\pm$ 0.27	3.66 $\pm$ 0.11	3.20 $\pm$ 0.11	3.33 $\pm$ 0.12	2.42 $\pm$ 0.12	-
A stem	1.14	3.83 $\pm$ 0.07	4.28 $\pm$ 0.29	4.35 $\pm$ 0.10	4.74 $\pm$ 0.15	3.99 $\pm$ 0.12	3.67 $\pm$ 0.12
B stem	-	1.39 $\pm$ 0.01	2.98 $\pm$ 0.15	3.49 $\pm$ 0.22	3.90 $\pm$ 0.70	3.68 $\pm$ 0.27	3.31 $\pm$ 0.16
Top	-	-	1.43 $\pm$ 0.11	1.87 $\pm$ 0.12	2.53 $\pm$ 0.25	1.87 $\pm$ 0.14	0.48 $\pm$ 0.03
Pods	-	0.60 $\pm$ 0.19	1.68 $\pm$ 0.19	3.04 $\pm$ 0.07	4.83 $\pm$ 0.10	4.12 $\pm$ 0.06	3.43 $\pm$ 0.10
Seeds	-	-	-	1.21 $\pm$ 0.14	7.08 $\pm$ 0.31	10.87 $\pm$ 0.26	14.14 $\pm$ 0.26
Root	1.00	2.34 $\pm$ 0.02	2.72 $\pm$ 0.08	3.13 $\pm$ 0.09	3.88 $\pm$ 0.09	3.27 $\pm$ 0.06	3.42 $\pm$ 0.13
Total	3.78	12.46 $\pm$ 1.08	17.73 $\pm$ 0.60	21.22 $\pm$ 0.72	30.97 $\pm$ 0.30	30.84 $\pm$ 0.87	28.45 $\pm$ 0.81

¹⁾ No roots harvested, weight estimated from other plants.

²⁾ A = the first 5-6 nodes (pure vegetative)
B = nodes in the mid-region of the plant (all nodes with pods)

Table 2.4 Dry matter (g) of field bean plant parts after various harvesting times during 1975. Mean $\pm$ S.E., n = 6-18.

Decapitated Skladia

Harvest date	17.6	3.7	10.7	17.7	31.7	19.8
Leaves	3.10	5.35 $\pm$ 0.70	6.30 $\pm$ 0.23	6.33 $\pm$ 0.53	5.26 $\pm$ 0.28	0.75 $\pm$ 0.03
Stem	0.91	5.63 $\pm$ 0.13	8.22 $\pm$ 0.44	9.30 $\pm$ 0.39	8.25 $\pm$ 0.34	7.04 $\pm$ 0.23
Pods	-	0.95 $\pm$ 0.05	2.20 $\pm$ 0.21	4.69 $\pm$ 0.23	6.83 $\pm$ 0.30	4.72 $\pm$ 0.22
Seeds	-	-	-	1.01 $\pm$ 0.06	9.18 $\pm$ 0.64	17.65 $\pm$ 1.11
Root	1.00 ¹⁾	4.17 $\pm$ 0.14	6.63 $\pm$ 0.14	6.07 $\pm$ 0.25	7.12 $\pm$ 0.24	9.41 $\pm$ 0.66
Total	5.01	16.14 $\pm$ 1.25	23.43 $\pm$ 0.70	27.77 $\pm$ 1.34	36.63 $\pm$ 1.26	39.07 $\pm$ 1.70

Sv 0621

Harvest date	13.6	1.7	8.7	15.7	29.7	15.8
Leaves	2.51	6.17 $\pm$ 1.08	5.17 $\pm$ 0.35	5.28 $\pm$ 0.17	5.03 $\pm$ 0.22	1.88 $\pm$ 0.27
Stem	0.46	6.93 $\pm$ 0.43	8.18 $\pm$ 0.41	8.77 $\pm$ 0.33	7.89 $\pm$ 0.38	6.30 $\pm$ 0.38
Lateral branches 2)	-	-	2.62 $\pm$ 0.89	2.43 $\pm$ 0.24	1.70 $\pm$ 0.26	3.14 $\pm$ 0.48
Pods	-	1.34 $\pm$ 0.42	4.28 $\pm$ 0.24	5.66 $\pm$ 0.30	6.89 $\pm$ 0.08	4.93 $\pm$ 0.17
Seeds	-	-	-	1.65 $\pm$ 0.20	8.32 $\pm$ 0.34	15.28 $\pm$ 0.65
Root	1.00	4.64 $\pm$ 0.24	5.31 $\pm$ 0.15	5.83 $\pm$ 0.09	5.82 $\pm$ 0.27	8.33 $\pm$ 0.72
Total	3.97	19.07 $\pm$ 0.22	25.56 $\pm$ 1.33	29.62 $\pm$ 0.52	35.72 $\pm$ 0.58	39.88 $\pm$ 1.34

1) No roots harvested, weight estimated from other plants.

2) All branches except the two that were treated together as the main shoot.

Figures 2.1 a-d show dry matter accumulation in vegetative and reproductive material. In 1973 Primus was about 2-3 days earlier than Skladia with regard to vegetative growth. Reproductive growth was at first comparable with regard to timing and intensity. However, during seed filling Primus showed a higher growth rate, but since the filling period was shorter in Primus than in Skladia the final reproductive dry matter did not differ. The effective filling period duration (EFPD), i.e. the seed yield divided by the reproductive growth rate, was calculated to 23.8 days in Primus and 27.5 days in Skladia. The reproductive growth rate used was that between 20% to 80% of the final reproductive material.

In 1975 initial flowering of Skladia occurred 8-9 days later than in 1973 and initial pod set about 4 days later. Before decapitation the growth rate was nearly similar in 1973 and 1975. However, after decapitation the rate of dry matter accumulation was higher in decapitated plants as compared with intact Skladia plants at stages IV and V in 1975 (Fig. 2.1.c.). EFPD was 24.2 days.

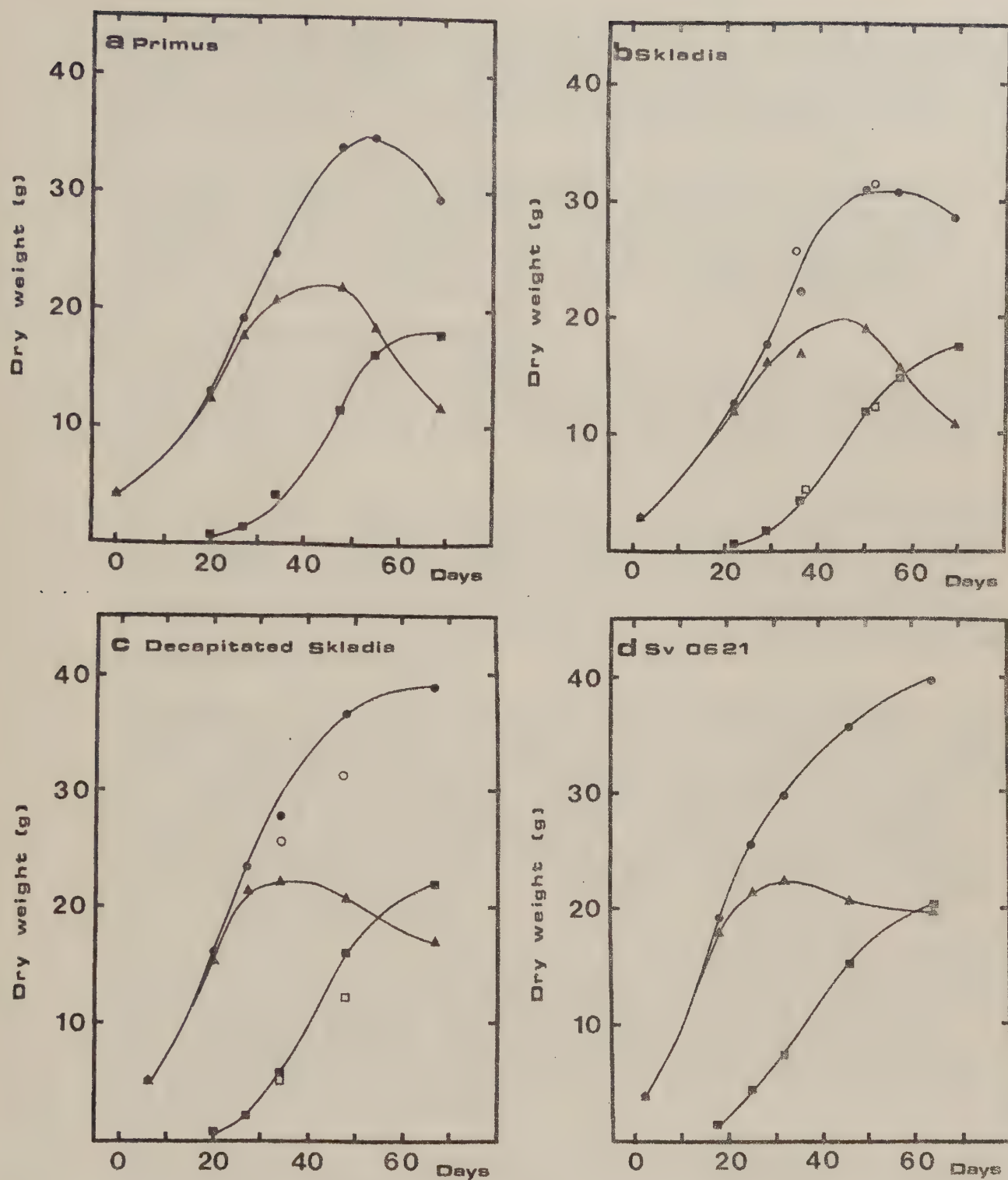


Fig. 2.1 a-d Dry matter accumulation in vegetative and reproductive material from initial flowering until maturity.
 ● Total dry matter. ▲ Vegetative dry matter.
 ■ Reproductive dry matter (pods and seeds).
 ○, □ Total and reproductive dry matter of non-decapitated Skladia plants from 1975. Fig. a, b are from 1973 and c, d from 1975.

The comparison of total dry matter accumulation in 1973 and 1975, however, is complicated by the root weights which in 1975 were higher because of another technique that was used and which reduced the loss of root material during washing. The reproductive dry matter, however, was not affected.

In Sv 0621 initial pod filling started 1-2 days earlier than in the decapitated Skladia. Reproductive growth was at first faster, but at the time of rapid seed growth it was slower than in the decapitated Skladia. EFPD was 29 days, but in spite of this the yield per plant was only 15.3 g, as compared with 17.2 g for decapitated Skladia.

2.4.2 Distribution of ^{14}C -assimilates

Tables 2.5-2.9 show the distribution of ^{14}C -assimilates in plants after various time periods following $^{14}\text{CO}_2$ assimilation. To facilitate interpretation the results of Primus have also been presented in histogram form in Figure 2.2.

When plants were allowed to assimilate $^{14}\text{CO}_2$ during the vegetative growth period (stage I), prior to initial flowering, most activity was recovered after 20 days in expanding leaves of zone B and in the stem of zone A (Table 2.5 and Figure 2.2). As the plants grew older the ^{14}C -activity in leaves decreased, while it remained practically constant in the stem. During the last weeks just prior to maturity, some labelled material was re-translocated to the seeds.

The amount of ^{14}C translocated to the roots during the first hour after treatment was not measured. However, in soybeans ^{14}C recovered in roots after a translocation time of one hour was 4% of the total if the plants were treated prior to flowering. Treatment during pod and seed filling stages resulted in a decreased translocation to the roots (Hume and Criswell 1973). In the present study ^{14}C recovered in roots after a translocation time of more than one week was at maximum 11.6% of the initial assimilated ^{14}C . This value decreased slightly with the length of the translocation period.

Treatment at early pod development (stage II) resulted in the accumulation of ^{14}C during the first week in both stems A and B and in the top zone that was developing. At this stage pods were also sinks but as seed development started, re-translocation of ^{14}C to the seeds from leaves and stem and pods occurred (Table 2.6, Fig. 2.2). Activity in the root was doubled as compared to that at stage I, but as percentage of initial ^{14}C , it was decreased.

The fact that more ^{14}C accumulated in the stem of zone A in Primus and that more was recovered in the seeds of Skladia, constitute the main difference between the two varieties. This could be a result of different sink activity in pods because of the earlier pod set in Skladia.

At late pod development (stage III) zone B and the top zone were the most important sources of assimilates. Pods and later seeds were acting as strong sinks. One week after treatment 22% and 35% of initial ^{14}C was recovered in pods of Primus and Skladia, respectively. Furthermore, at this time the stem of zone A also seemed to be a temporary sink. However, this pool was used to fill the seed two to three weeks later. Other parts that showed declining ^{14}C -activity were the leaves, especially the leaves of the top zone (Table 2.7).

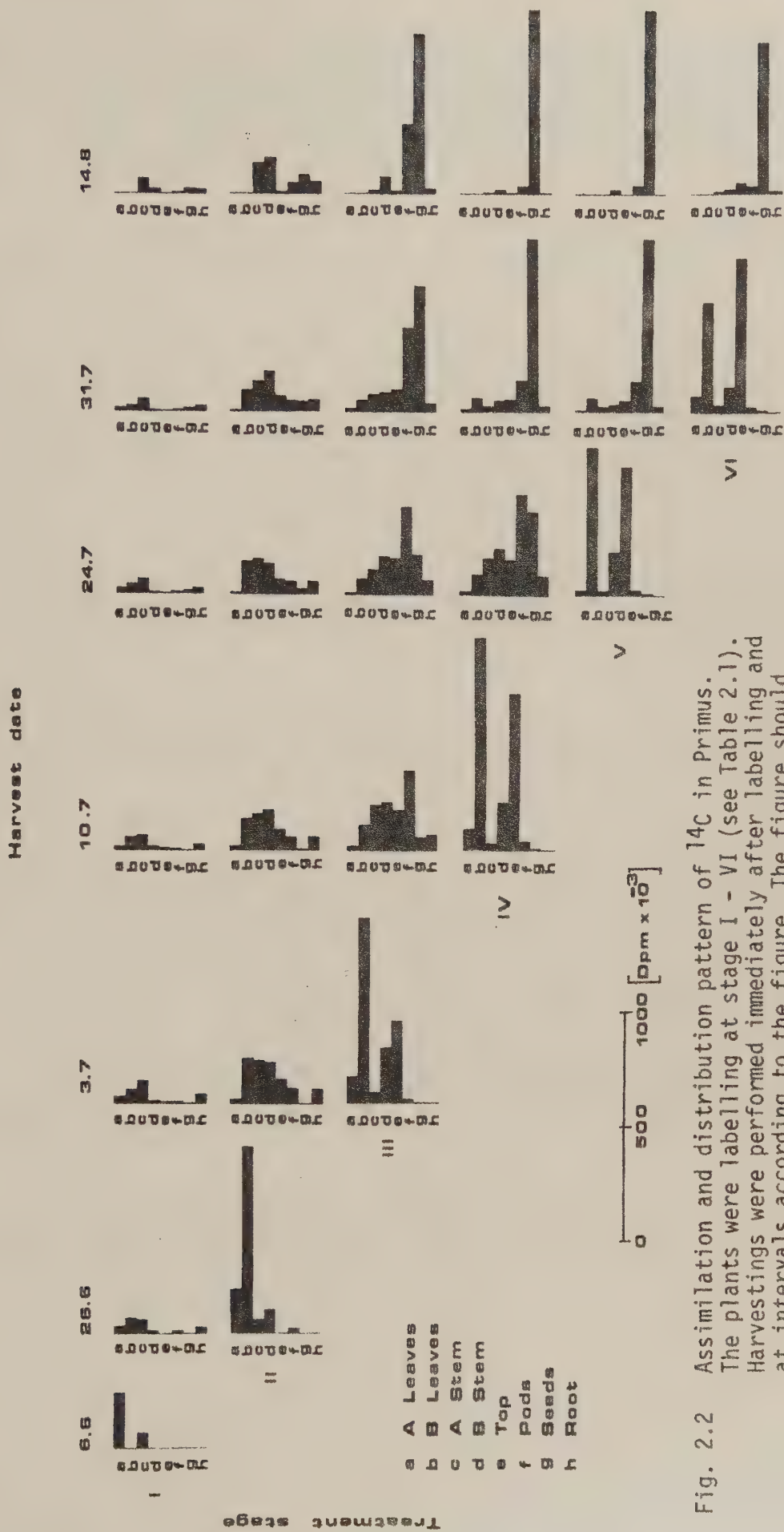


Fig. 2.2 Assimilation and distribution pattern of ^{14}C in *Primus*.
 The plants were labelling at stage I - VI (see Table 2.1).
 Harvestings were performed immediately after labelling and
 at intervals according to the figure. The figure should
 only be read horizontally.

Table 2.5 Distribution of radioactivity in field bean plant after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage I, initiation of flowering. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$). b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

PRIMUS

Harvest date	6.6		26.6		3.7		10.7		24.7		31.7		14.8	
Days between labelling and harvest	0		20		27		34		48		55		69	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
A leaf ¹⁾	239	79.0	28 $\pm$ 2	9.3	30 $\pm$ 2	9.9	16 $\pm$ 6	5.3	25 $\pm$ 4	8.3	15 $\pm$ 5	5.1	-	-
B leaf	-	-	69 $\pm$ 2	22.7	58 $\pm$ 14	19.2	55 $\pm$ 5	18.3	43 $\pm$ 3	14.3	24 $\pm$ 3	7.8	-	-
A stem	64	21.0	60 $\pm$ 2	19.9	95 $\pm$ 13	31.1	64 $\pm$ 2	21.0	69 $\pm$ 2	22.7	59 $\pm$ 3	19.3	66 $\pm$ 4	21.8
B stem	-	-	9 $\pm$ 2	3.0	9 $\pm$ 2	3.0	14 $\pm$ 3	4.5	9 $\pm$ 2	3.0	8 $\pm$ 3	2.8	17 $\pm$ 4	5.4
Top	-	-	-	-	4 $\pm$ 0	1.2	4 $\pm$ 1	1.3	4 $\pm$ 0	1.1	2 $\pm$ 0	0.6	1 $\pm$ 0	0.4
Pods	-	-	5 $\pm$ 1	1.5	5 $\pm$ 1	1.8	7 $\pm$ 0	2.4	9 $\pm$ 0	2.8	8 $\pm$ 1	2.5	5 $\pm$ 0	1.8
Seeds	-	-	-	-	-	-	1 $\pm$ 1	0.5	8 $\pm$ 1	2.7	14 $\pm$ 2	4.7	22 $\pm$ 0	7.2
Root	-	-	21 $\pm$ 2	7.0	34 $\pm$ 4	11.1	29 $\pm$ 2	9.2	26 $\pm$ 4	8.4	24 $\pm$ 2	7.9	20 $\pm$ 0	6.6
Total	303	100	192 $\pm$ 42	63.4	235 $\pm$ 26	77.3	190 $\pm$ 25	62.5	193 $\pm$ 2	63.3	154 $\pm$ 5	50.8	131 $\pm$ 4	43.2

SKLADIA

Harvest date	8.6		28.6		5.7		12.7		26.7		1.8		14.8	
Days between labelling and harvest	0		20		27		34		48		55		67	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
A leaves	257	79.1	33 $\pm$ 7	10.2	18 $\pm$ 2	5.5	33 $\pm$ 6	10.1	13 $\pm$ 2	4.2	9 $\pm$ 2	2.9	-	-
B leaves	-	-	66 $\pm$ 8	20.2	83 $\pm$ 4	25.8	50 $\pm$ 6	15.5	52 $\pm$ 5	15.9	28 $\pm$ 9	8.6	-	-
A stem	65	20.9	100 $\pm$ 8	30.6	94 $\pm$ 8	28.8	86 $\pm$ 8	26.5	95 $\pm$ 3	29.2	62 $\pm$ 6	19.1	64 $\pm$ 3	19.7
B stem	-	-	9 $\pm$ 3	2.7	20 $\pm$ 4	6.2	10 $\pm$ 2	3.3	18 $\pm$ 2	5.4	10 $\pm$ 1	3.2	9 $\pm$ 1	2.6
Top	-	-	-	-	4 $\pm$ 1	1.1	3 $\pm$ 0	0.8	6 $\pm$ 0	1.9	2 $\pm$ 0	0.6	0	0.1
Pods	-	-	5 $\pm$ 1	1.4	10 $\pm$ 1	3.0	8 $\pm$ 1	2.5	9 $\pm$ 0	2.7	6 $\pm$ 0	1.8	4 $\pm$ 0	1.1
Seeds	-	-	-	-	-	-	3 $\pm$ 1	0.8	12 $\pm$ 0	3.6	13 $\pm$ 1	4.0	16 $\pm$ 4	5.0
Root	-	-	28 $\pm$ 3	8.7	42 $\pm$ 4	11.6	30 $\pm$ 4	9.4	37 $\pm$ 6	11.5	28 $\pm$ 2	8.5	30 $\pm$ 1	9.1
Total	322	100	241 $\pm$ 59	73.8	270 $\pm$ 24	82.0	224 $\pm$ 20	68.9	241 $\pm$ 32	74.4	158 $\pm$ 18	48.7	122 $\pm$ 16	37.6

- ¹⁾ A = the first 5-6 nodes (pure vegetative)
 B = the nodes in the mid-region of the plant (all nodes with pods)

Table 2.6 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage II, early pod development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$). b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

PRIMUS

Harvest date	26.6		3.7		10.7		24.7		31.7		14.8	
Days between labelling and harvest	0		7		14		28		35		49	
	a	b	a	b	a	b	a	b	a	b	a	b
A leaves 1)	190 $\pm$ 28	16.1	20 $\pm$ 1	1.7	20 $\pm$ 3	1.7	9 $\pm$ 1	0.8	6 $\pm$ 2	0.5	-	-
B leaves	816 $\pm$ 38	69.3	196 $\pm$ 11	16.7	136 $\pm$ 1	11.6	144 $\pm$ 1	12.2	93 $\pm$ 9	7.9	-	-
A stem	56 $\pm$ 13	4.8	189 $\pm$ 54	16.1	159 $\pm$ 13	13.5	152 $\pm$ 21	12.9	131 $\pm$ 5	11.1	133 $\pm$ 34	11.3
B stem	102 $\pm$ 24	8.7	176 $\pm$ 23	15.0	173 $\pm$ 6	14.7	135 $\pm$ 16	11.5	176 $\pm$ 5	15.0	157 $\pm$ 6	13.3
Top	-	-	103 $\pm$ 19	8.8	90 $\pm$ 11	7.6	62 $\pm$ 10	5.3	61 $\pm$ 5	5.2	10 $\pm$ 3	0.8
Pods	13 $\pm$ 2	1.1	69 $\pm$ 20	5.9	58 $\pm$ 10	4.9	53 $\pm$ 6	4.5	45 $\pm$ 2	3.8	49 $\pm$ 18	4.2
Seeds	-	-	-	-	6 $\pm$ 1	0.5	21 $\pm$ 1	1.8	45 $\pm$ 4	3.8	81 $\pm$ 15	6.9
Root	-	-	57 $\pm$ 6	4.8	60 $\pm$ 8	5.1	58 $\pm$ 5	4.9	50 $\pm$ 2	4.2	56 $\pm$ 2	4.8
Total	1177 $\pm$ 133	100	809 $\pm$ 109	69.0	702 $\pm$ 29	59.6	634 $\pm$ 47	53.9	607 $\pm$ 9	51.6	486 $\pm$ 30	41.3

SKLADIA

Harvest date	28.6		5.7		12.7		26.7		1.8		14.8	
Days between labelling and harvest	0		7		14		28		35		47	
	a	b	a	b	a	b	a	b	a	b	a	b
A leaves	178 $\pm$ 5	19.6	24 $\pm$ 4	2.6	17 $\pm$ 7	1.9	9 $\pm$ 2	1.0	8 $\pm$ 1	0.9	-	-
B leaves	541 $\pm$ 6	59.6	190 $\pm$ 17	20.9	121 $\pm$ 19	13.3	126 $\pm$ 16	13.9	56 $\pm$ 4	6.2	-	-
A stem	89 $\pm$ 8	9.8	140 $\pm$ 13	15.4	83 $\pm$ 9	9.1	87 $\pm$ 5	9.6	62 $\pm$ 10	6.8	34 $\pm$ 4	3.7
B stem	91 $\pm$ 12	10.0	164 $\pm$ 10	18.1	100 $\pm$ 8	11.0	144 $\pm$ 6	15.9	95 $\pm$ 2	10.5	96 $\pm$ 1	10.6
Top	-	-	115 $\pm$ 27	12.7	115 $\pm$ 14	12.7	97 $\pm$ 16	10.7	68 $\pm$ 7	7.5	21 $\pm$ 8	2.3
Pods	9 $\pm$ 3	1.0	91 $\pm$ 16	10.0	56 $\pm$ 11	6.2	62 $\pm$ 4	6.8	73 $\pm$ 10	8.0	70 $\pm$ 16	7.7
Seeds	-	-	-	-	13 $\pm$ 3	1.4	33 $\pm$ 1	3.6	77 $\pm$ 12	8.5	114 $\pm$ 6	12.6
Root	-	-	67 $\pm$ 12	7.4	45 $\pm$ 3	5.0	47 $\pm$ 2	5.2	37 $\pm$ 5	4.1	39 $\pm$ 12	4.3
Total	908 $\pm$ 164	100	791 $\pm$ 57	87.1	550 $\pm$ 61	60.6	605 $\pm$ 35	66.6	476 $\pm$ 68	52.4	374 $\pm$ 27	41.2

- 1) A = the first 5-6 nodes (pure vegetative)
B = the nodes in the mid-region of the plant (all nodes with pods)

Table 2.7 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage III, late pod development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$). b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

PRIMUS

Harvest date	3.7		10.7		24.7		31.7		14.8	
Days between labelling and harvest	0		7		21		28		42	
	a	b	a	b	a	b	a	b	a	b
A leaves ¹⁾	115 $\pm$ 33	7.3	13 $\pm$ 1	0.8	7 $\pm$ 0	0.4	7 $\pm$ 2	0.4	-	-
B leaves	808 $\pm$ 82	50.9	121 $\pm$ 6	7.6	69 $\pm$ 15	4.4	40 $\pm$ 9	2.5	-	-
A stem	44 $\pm$ 8	2.8	199 $\pm$ 28	12.5	110 $\pm$ 7	6.9	81 $\pm$ 12	5.1	77 $\pm$ 9	4.9
B stem	241 $\pm$ 43	15.2	208 $\pm$ 25	13.1	170 $\pm$ 13	10.7	116 $\pm$ 19	7.3	163 $\pm$ 11	10.3
Top	360 $\pm$ 54	22.7	177 $\pm$ 24	11.2	157 $\pm$ 21	9.9	116 $\pm$ 24	7.3	36 $\pm$ 32	2.3
Pods	18 $\pm$ 5	1.1	344 $\pm$ 40	21.7	384 $\pm$ 10	24.2	337 $\pm$ 37	21.2	221 $\pm$ 32	13.9
Seeds	-	-	53 $\pm$ 12	3.3	178 $\pm$ 30	11.2	281 $\pm$ 17	17.7	261 $\pm$ 18	16.5
Root	-	-	64 $\pm$ 6	4.0	66 $\pm$ 15	4.2	36 $\pm$ 2	2.3	32 $\pm$ 3	2.0
Total	1586 $\pm$ 68	100	1179 $\pm$ 136	74.3	1141 $\pm$ 83	71.9	1014 $\pm$ 152	63.9	790 $\pm$ 103	49.8

SKLADIA

Harvest date	5.7		12.7		26.7		1.8		14.8	
Days between labelling and harvest	0		7		21		28		40	
	a	b	a	b	a	b	a	b	a	b
A leaves	137 $\pm$ 22	10.6	24 $\pm$ 5	1.9	7 $\pm$ 2	0.5	11.2	0.9	-	-
B leaves	621 $\pm$ 35	48.2	97 $\pm$ 7	7.5	57 $\pm$ 8	4.4	35 $\pm$ 3	2.7	-	-
A stem	77 $\pm$ 10	6.0	116 $\pm$ 34	9.0	60 $\pm$ 12	4.7	49 $\pm$ 11	3.8	40 $\pm$ 9	3.1
B stem	156 $\pm$ 37	12.1	109 $\pm$ 4	8.5	80 $\pm$ 14	6.2	62 $\pm$ 4	4.8	65 $\pm$ 12	5.0
Top	281 $\pm$ 21	21.8	163 $\pm$ 31	12.6	96 $\pm$ 4	7.4	75 $\pm$ 13	5.8	21 $\pm$ 5	1.6
Pods	17 $\pm$ 6	1.3	453 $\pm$ 18	35.1	319 $\pm$ 10	24.9	260 $\pm$ 8	20.2	184 $\pm$ 15	14.3
Seeds	-	-	169 $\pm$ 48	13.1	181 $\pm$ 26	14.0	240 $\pm$ 3	18.6	245 $\pm$ 15	19.0
Root	-	-	57 $\pm$ 8	4.4	31 $\pm$ 1	2.4	34 $\pm$ 3	2.6	32 $\pm$ 4	2.5
Total	1289 $\pm$ 233	100	1188 $\pm$ 216	92.2	831 $\pm$ 71	64.5	766 $\pm$ 5	59.4	587 $\pm$ 53	45.5

- ¹⁾ A = the first 5-6 nodes (pure vegetative)
B = nodes in the mid-region of the plant (all nodes with pods)

Table 2.8 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage IV, early seed development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$), b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

PRIMUS

Harvest date	10.7		24.7		31.7		14.8	
Days between labelling and harvest	0		14		21		35	
	a	b	a	b	a	b	a	b
A leaves ¹⁾	95 $\pm$ 14	4.8	13 $\pm$ 5	0.7	10 $\pm$ 1	0.5	-	-
B leaves	921 $\pm$ 85	46.5	90 $\pm$ 9	4.5	49 $\pm$ 1	2.5	-	-
A stem	30 $\pm$ 8	1.5	159 $\pm$ 21	8.0	77 $\pm$ 14	3.9	19 $\pm$ 7	1.0
B stem	210 $\pm$ 42	10.6	202 $\pm$ 39	10.2	80 $\pm$ 10	4.0	76 $\pm$ 6	3.8
Top	680 $\pm$ 46	34.3	155 $\pm$ 20	7.8	94 $\pm$ 10	4.7	15 $\pm$ 10	0.8
Pods	39 $\pm$ 16	2.0	441 $\pm$ 50	22.3	361 $\pm$ 49	18.2	305 $\pm$ 17	15.4
Seeds	6 $\pm$ 4	0.3	364 $\pm$ 105	18.4	547 $\pm$ 78	27.6	700 $\pm$ 21	35.3
Root	-	-	83 $\pm$ 9	4.2	38 $\pm$ 8	1.9	28 $\pm$ 1	1.4
Total	1981 $\pm$ 169	100	1507 $\pm$ 59	76.1	1256 $\pm$ 31	63.4	1143 $\pm$ 119	57.7

SKLADIA

Harvest date	12.7		26.7		1.8		14.8	
Days between labelling and harvest	0		14		21		33	
	a	b	a	b	a	b	a	b
A leaves	80 $\pm$ 12	6.0	7 $\pm$ 1	0.5	9 $\pm$ 3	0.7	-	-
B leaves	640 $\pm$ 47	47.9	77 $\pm$ 4	5.8	45 $\pm$ 11	3.4	-	-
A stem	44 $\pm$ 13	3.3	96 $\pm$ 7	7.2	81 $\pm$ 10	6.1	41 $\pm$ 10	3.1
B stem	214 $\pm$ 29	16.0	67 $\pm$ 5	5.0	74 $\pm$ 13	5.5	48 $\pm$ 7	3.6
Top	307 $\pm$ 31	23.0	68 $\pm$ 4	5.1	60 $\pm$ 5	4.5	8 $\pm$ 1	0.6
Pods	43 $\pm$ 7	3.2	327 $\pm$ 20	24.5	281 $\pm$ 17	21.0	214 $\pm$ 38	16.0
Seeds	9 $\pm$ 3	0.7	498 $\pm$ 21	37.2	348 $\pm$ 21	26.0	508 $\pm$ 47	38.0
Root	-	-	41 $\pm$ 2	3.1	35 $\pm$ 4	2.6	22 $\pm$ 3	1.6
Total	1337 $\pm$ 53	100	1181 $\pm$ 41	88.3	933 $\pm$ 119	69.8	841 $\pm$ 105	62.9

- ¹⁾ A = the first 5-6 nodes (pure vegetative)
 B = nodes in the mid-region of the plant (all nodes with pods)

Table 2.9 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage V, rapid seed development. Stage VI late seed development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$); b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

PRIMUS

Harvest date	Stage V						Stage VI			
	24.7		31.7		14.8		31.7		14.8	
	0		7		21		0		14	
Days between labelling and harvest	a	b	a	b	a	b	a	b	a	b
A leaves ¹⁾	26 $\pm$ 10	1.8	11 $\pm$ 2	0.7	-	-	71 $\pm$ 29	5.1	-	-
B leaves	649 $\pm$ 1	43.7	61 $\pm$ 1	4.1	-	-	480 $\pm$ 45	34.4	-	-
A stem	22 $\pm$ 3	1.5	23 $\pm$ 2	1.6	6 $\pm$ 1	0.4	25 $\pm$ 7	1.8	11 $\pm$ 2	0.8
B stem	192 $\pm$ 37	12.9	48 $\pm$ 4	3.2	20 $\pm$ 3	1.3	112 $\pm$ 17	8.0	20 $\pm$ 2	1.4
Top	566 $\pm$ 59	38.1	49 $\pm$ 12	3.3	6 $\pm$ 2	0.4	673 $\pm$ 80	48.2	45 $\pm$ 2	3.2
Pods	23 $\pm$ 4	1.5	135 $\pm$ 7	9.1	36 $\pm$ 11	2.4	25 $\pm$ 3	1.8	36 $\pm$ 13	2.6
Seeds	7 $\pm$ 1	0.5	754 $\pm$ 15	50.8	801 $\pm$ 15	53.9	11 $\pm$ 1	0.8	660 $\pm$ 28	47.2
Root	-	-	25 $\pm$ 3	1.7	6 $\pm$ 2	0.4	-	-	19 $\pm$ 8	1.4
Total	1485 $\pm$ 235		1106 $\pm$ 88	74.5	875 $\pm$ 76	58.9	1396 $\pm$ 114	100	791 $\pm$ 61	56.6

SKLADIA

Harvest date	Stage V						Stage VI			
	26.7		1.8		14.8		1.8		14.8	
	0		7		19		0		12	
Days between labelling and harvest	a	b	a	b	a	b	a	b	a	b
A leaves ¹⁾	75 $\pm$ 12	5.5	10 $\pm$ 1	0.7	-	-	3(8)3)	0.7	-	-
B leaves	625 $\pm$ 50	45.4	50 $\pm$ 3	3.6	-	-	164(398)	30.7	-	-
A stem	32 $\pm$ 7	2.3	18 $\pm$ 4	1.3	17 $\pm$ 8	1.2	6(15)	1.1	10 $\pm$ 2	0.8
B stem	186 $\pm$ 37	13.5	27 $\pm$ 3	2.0	28 $\pm$ 6	2.0	64(156)	11.9	15 $\pm$ 2	1.2
Top	422 $\pm$ 17	30.7	26 $\pm$ 3	1.9	9 $\pm$ 4	0.7	285(693)	53.3	4 $\pm$ 1	0.3
Pods	22 $\pm$ 6	1.6	76 $\pm$ 11	5.5	84 $\pm$ 26	6.1	6(15)	1.1	3 $\pm$ 6	0.2
Seeds	14 $\pm$ 6	1.0	509 $\pm$ 22	37.0	858 $\pm$ 51	62.4	6(15)	1.1	733 $\pm$ 12	56.4
Root	-	-	23 $\pm$ 4	1.7	16 $\pm$ 7	1.2	-	-	15 $\pm$ 2	1.2
Total	1376 $\pm$ 218	100	739 $\pm$ 72	53.7	1012 $\pm$ 52	73.5	534 $\pm$ 56	100	780 $\pm$ 34	60.0 ²⁾

1) A = the first 5-6 nodes (pure vegetative)

B = the nodes in the mid-region of the plant (all nodes with pods)

2) Far too low a value as compared with Primus; a more probable value is 1300 $\times 10^{-3}$ dpm.

3) In brackets values re-calculated using 1300 $\times 10^{-3}$ dpm.

As in the treatment of stage II the somewhat earlier and more intense growth of pods and seeds increased the amount of ^{14}C translocated to Skladia seeds one week after treatment. At maturity this difference between Primus and Skladia was reduced.

During the stage of early seed development (stage IV) the leaves of zone B and those of the top zone were still more dominating as sources of assimilate than those in the earlier stages (Tables 2.8 and Fig. 2.2). Pods and seeds were major sinks but there was still a temporary accumulation in the lower stem. This different behaviour of zone A and B as sinks of assimilate could be explained by the position of the pods. During stages III and IV the pods started to act as strong sinks and since they were situated at the stem of zone B, more assimilate came from this part, and translocation of assimilate from zone A was delayed.

At the stage of the rapid seed development (stage V and VI) about 50% of the initial ^{14}C was recovered in seeds one week after treatment (Table 2.9) and at harvesting two weeks later, almost all recovered activity was found in the seeds.

Losses of ^{14}C assimilated at the first three stages occurred in two phases (Fig. 2.3 and Tables 2.5-2.9); a rapid phase, where about 25% of the ^{14}C -labelled assimilate was lost until the next harvest, and a second, slower phase that continued until maturity. During this latter phase ^{14}C was lost at the rate of 0.5-0.7% a day.

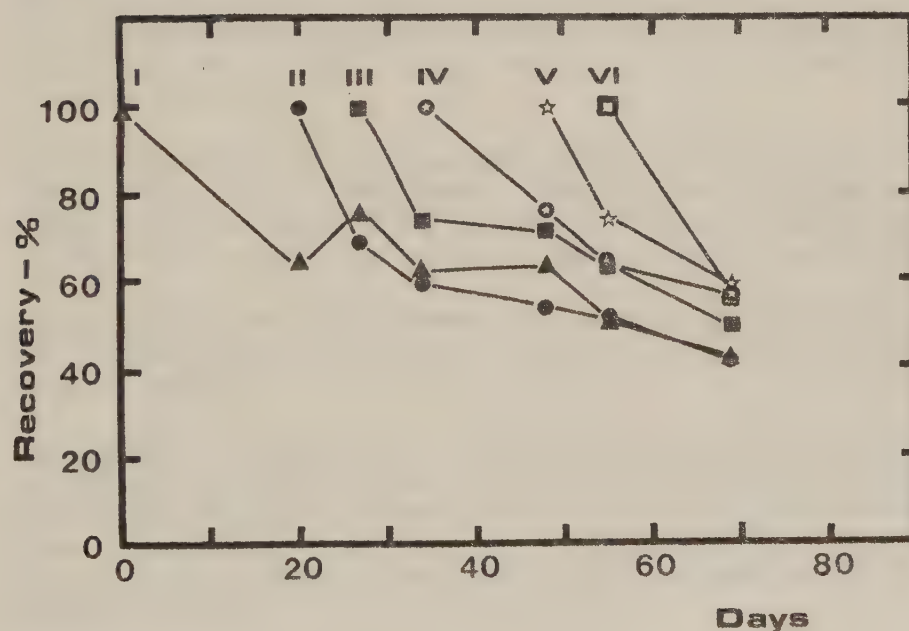


Fig. 2.3 Recovery percentage after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants of Primus. I-VI denotes stages of development and labelling according to Table 2.1. Day 0, initial flowering.

Losses of ^{14}C assimilated during the last three stages occurred principally in the rapid phase. On average, (phase 1 and phase 2 together) losses occurred with an increasing rate from 1.2 to 3.2%. Comparable average rates at stage I to III were 0.8 to 1.2%. At maturity, about 60% of the early fixed ^{14}C was lost as compared to about 30-40% of late fixed ^{14}C in *Primus* and *Skladia*. There were no significant differences between *Primus* and *Skladia*.

Tables 2.10-2.13 show the distribution of radioactivity in decapitated plants of *Skladia* and in Sv 0621 after various time periods following $^{14}\text{CO}_2$ assimilation. In this experiment zone A and zone B were pooled together, and in Sv 0621 the first two developed branches were treated as a main shoot. The rest of the branches were smaller and usually did not set pods. They are referred to as laterals.

When plants assimilated $^{14}\text{CO}_2$ during vegetative growth (stage I), most ^{14}C was recovered in the vegetative parts of the plant (Table 2.10). Very little of the early fixed ^{14}C was used during growth of the top zone of *Skladia* or in lateral branches of Sv 0621. At pod filling 10 and 8% of initially assimilated ^{14}C was re-translocated to the seeds of *Skladia* and Sv 0621, respectively.

At early pod development (stage II) the stems and roots of *Skladia* were more active as sinks than those of Sv 0621 (Table 2.11). In Sv 0621 the development of lateral branches gave an alternative sink that possibly interfered with the supply of assimilate to the root. It is also evident that accumulated ^{14}C in the stem is re-translocated to the seeds during the rapid seed filling period.

One week after treatment, during late pod development (stage III), pods were the most active sinks for assimilate (Table 2.12). During seed growth, assimilate was translocated from pods, leaves and stems to the seeds. In Sv 0621 lateral branches may also have contributed assimilate to the seeds.

^{14}C fixed during early seed development (stage IV) was recovered two weeks later in pods and seeds. Translocation to seeds in Sv 0621 occurred faster than in decapitated *Skladia*. In decapitated *Skladia* more ^{14}C was accumulated in pods and only at maturity recovered in the seeds.

During rapid seed development, 53 and 63% of initial assimilated ^{14}C was recovered at maturity in seeds of decapitated *Skladia* and Sv 0621, respectively.

The losses of assimilate in decapitated *Skladia* and in Sv 0621 followed a similar pattern as shown in Fig. 2.3. Average rates of losses ranged from 0.8-1.8%. Early fixed ^{14}C was lost to a greater extent in Sv 0621 than in decapitated *Skladia*. Late assimilated ^{14}C , on the other hand, was lost to a lesser extent in Sv 0621 as compared to that in decapitated *Skladia*.

2.5 Discussion

The assimilation and distribution patterns of assimilate in *Primus* and *Skladia* are with few exceptions identical. The small divergencies can be attributed to the increased vegetative growth in *Primus*. This affected total assimilation but probably also the development of pods and seeds. However, as in several other similar cases, it is not possible to

Table 2.10 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage I, initiation of flowering. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$); b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

Decapitated SKALDIA ¹⁾

Harvest date	17.6		3.7		10.7		17.7		31.7		19.8	
Days between treatment and harvest	0		16		23		30		44		64	
	a	b	a	b	a	b	a	b	a	b	a	b
Leaves	343 $\pm$ 3	94.9	125 $\pm$ 7	34.7	99 $\pm$ 5	27.3	107 $\pm$ 5	29.6	65 $\pm$ 4	18.0	6 $\pm$ 1	1.7
Stem	19 $\pm$ 3	5.1	96 $\pm$ 5	26.6	78 $\pm$ 5	21.5	88 $\pm$ 6	24.4	58 $\pm$ 2	16.1	70 $\pm$ 7	19.3
Top ²⁾	-	-	2 $\pm$ 1	0.5	1 $\pm$ 0	0.3	1 $\pm$ 0	0.4	3 $\pm$ 1	0.7	1 $\pm$ 0	0.4
Pods	-	-	13 $\pm$ 13	3.5	10 $\pm$ 1	2.8	11 $\pm$ 0	2.9	10 $\pm$ 2	2.8	8 $\pm$ 0	2.2
Seeds	-	-	-	-	-	-	2 $\pm$ 0	0.6	12 $\pm$ 1	3.4	38 $\pm$ 2	10.4
Root	-	-	37 $\pm$ 2	10.3	37 $\pm$ 3	10.4	26 $\pm$ 1	7.2	26 $\pm$ 2	7.1	32 $\pm$ 0.3	8.8
Total	362 $\pm$ 17	100	273 $\pm$ 12	75.6	225 $\pm$ 13	62.2	236 $\pm$ 24	65.2	174 $\pm$ 8	48.2	154 $\pm$ 40	42.7

Sv 0621

Harvest date	13.6		1.7		8.7		15.7		29.7		16.8	
Days between treatment and harvest	0		18		25		32		46		64	
	a	b	a	b	a	b	a	b	a	b	a	b
Leaves	325 $\pm$ 1	97.7	116 $\pm$ 7	35.0	103 $\pm$ 9	30.7	98 $\pm$ 3	29.5	70 $\pm$ 2	21.0	19 $\pm$ 3	5.9
Stem	8 $\pm$ 1	2.3	66 $\pm$ 7	19.9	55 $\pm$ 3	16.6	52 $\pm$ 1	15.6	40 $\pm$ 2	11.9	41 $\pm$ 4	12.3
Lateral ³⁾ branches	-	-	-	-	11 $\pm$ 3	3.2	4 $\pm$ 0	1.2	3 $\pm$ 0	0.9	2 $\pm$ 1	0.7
Pods	-	-	7 $\pm$ 1	2.0	10 $\pm$ 1	2.9	12 $\pm$ 1	3.6	9 $\pm$ 2	2.8	8 $\pm$ 1	2.3
Seeds	-	-	-	-	-	-	3 $\pm$ 0	1.0	12 $\pm$ 0	3.5	25 $\pm$ 1	7.6
Root	-	-	30 $\pm$ 3	8.9	32 $\pm$ 4	9.8	25 $\pm$ 3	7.4	22 $\pm$ 2	6.7	24 $\pm$ 1	7.4
Total	333 $\pm$ 40	100	219 $\pm$ 26	65.8	211 $\pm$ 16	63.2	194 $\pm$ 24	58.4	156 $\pm$ 10	46.8	120 $\pm$ 16	36.2

- 1) No top zone developed at labelling time.
- 2) All top zones were removed on 3rd July.
- 3) All branches except the two that were treated together as the main shoot.

Table 2.11 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage II, early pod development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$), b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

Decapitated SKLADIA¹⁾

Harvest date	3.7		10.7		17.7		31.7		19.8	
Days between treatment and harvest	0		7		14		28		47	
	a	b	a	b	a	b	a	b	a	b
Leaves	680 $\pm$ 11	72.5	227 $\pm$ 27	24.2	210 $\pm$ 19	22.4	146 $\pm$ 12	15.6	20 $\pm$ 3	2.1
Stem	248 $\pm$ 9	26.4	341 $\pm$ 29	36.4	362 $\pm$ 35	38.6	297 $\pm$ 10	31.7	225 $\pm$ 5	24.0
Pods	10 $\pm$ 3	1.0	75 $\pm$ 9	8.0	75 $\pm$ 5	8.0	85 $\pm$ 15	9.1	48 $\pm$ 4	5.1
Seeds	-	-	-	-	11 $\pm$ 2	1.1	63 $\pm$ 8	6.7	119 $\pm$ 5	12.7
Root	-	-	114 $\pm$ 11	12.2	93 $\pm$ 9	9.9	104 $\pm$ 14	11.1	92 $\pm$ 7	9.8
Total	938 $\pm$ 85	100	758 $\pm$ 30	80.9	750 $\pm$ 47	80.0	696 $\pm$ 28	74.2	504 $\pm$ 25	53.7

Sv 0621

Harvest date	1.7		8.7		15.7		29.7		16.8	
Days between labelling and harvest	0		7		14		28		46	
	a	b	a	b	a	b	a	b	a	b
Leaves	640 $\pm$ 22	77.2	149 $\pm$ 9	18.0	113 $\pm$ 12	13.7	82 $\pm$ 1	9.9	26 $\pm$ 5	3.1
Stems	167 $\pm$ 22	20.2	193 $\pm$ 45	23.3	143 $\pm$ 15	17.3	151 $\pm$ 1	18.3	79 $\pm$ 11	9.5
Lateral ²⁾ branches	-	-	56 $\pm$ 53	6.8	102 $\pm$ 9	12.3	67 $\pm$ 35	8.1	64 $\pm$ 12	7.7
Pods	22 $\pm$ 10	2.6	91 $\pm$ 5	10.9	79 $\pm$ 22	9.5	90 $\pm$ 18	10.9	47 $\pm$ 4	5.7
Seeds	-	-	-	-	15 $\pm$ 3	1.8	61 $\pm$ 10	7.3	77 $\pm$ 10	9.3
Root	-	-	54 $\pm$ 3	6.5	46 $\pm$ 2	5.6	56 $\pm$ 11	6.8	23 $\pm$ 3	2.7
Total	828 $\pm$ 93	100	543 $\pm$ 46	65.6	498 $\pm$ 40	60.1	508 $\pm$ 33	61.3	316 $\pm$ 27	38.0

¹⁾ The plants were decapitated prior to labelling.

²⁾ All branches except the two that were treated together as the main shoot.

Table 2.12 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage III, late pod development. a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$, b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., n = 3.

Decapitated SKLADIA¹⁾

Harvest date	10.7		17.7		31.7		19.8	
Days between labelling and harvest	0		7		21		40	
	a	b	a	b	a	b	a	b
Leaves	924 $\pm$ 49	75.2	145 $\pm$ 25	11.8	92 $\pm$ 21	7.5	9 $\pm$ 1	0.7
Stem	290 $\pm$ 47	23.6	195 $\pm$ 18	15.9	147 $\pm$ 25	11.9	113 $\pm$ 2	9.2
Pods	14 $\pm$ 4	1.2	312 $\pm$ 42	25.4	297 $\pm$ 21	24.2	154 $\pm$ 15	12.5
Seeds	-	-	54 $\pm$ 14	4.4	139 $\pm$ 26	11.3	238 $\pm$ 20	19.3
Root	-	-	75 $\pm$ 14	6.1	55 $\pm$ 6	4.5	76 $\pm$ 5	6.2
Total	1228 $\pm$ 91	100	781 $\pm$ 135	63.6	730 $\pm$ 69	59.4	590 $\pm$ 46	48.0

Sv 0621

Harvest date	8.7		15.7		29.7		16.8	
Days between labelling and harvest	0		7		21		39	
	a	b	a	b	a	b	a	b
Leaves	636 $\pm$ 38	67.1	136 $\pm$ 21	14.3	82 $\pm$ 12	8.6	24 $\pm$ 6	2.5
Stems	166 $\pm$ 33	17.5	158 $\pm$ 19	16.7	84 $\pm$ 13	8.9	63 $\pm$ 14	6.6
Lateral ²⁾ branches	104 $\pm$ 61	10.9	103 $\pm$ 14	10.9	26 $\pm$ 9	2.7	56 $\pm$ 15	5.9
Pods	42 $\pm$ 8	4.5	288 $\pm$ 30	30.4	272 $\pm$ 11	28.7	190 $\pm$ 4	20.0
Seeds	-	-	73 $\pm$ 19	7.7	140 $\pm$ 15	14.8	276 $\pm$ 35	29.1
Root	-	-	36 $\pm$ 16	3.8	26 $\pm$ 1	2.7	22 $\pm$ 5	2.3
Total	948 $\pm$ 52	100	794 $\pm$ 73	83.8	630 $\pm$ 25	66.5	631 $\pm$ 51	66.5

¹⁾ Plants decapitated on 3rd July.

²⁾ All branches except the two that were treated together as the main shoot.

Table 2.13 Distribution of radioactivity in field bean plant parts after various time periods following $^{14}\text{CO}_2$ assimilation by whole plants. Stage IV, early seed development, Stage V, rapid seed development.
 a = recovered $^{14}\text{CO}_2$ (dpm $\times 10^{-3}$); b = % of total initial ^{14}C in each plant part. Mean $\pm$ S.E., $n = 3$.

Decapitated SKLADIA 1)

Stage IV							Stage V			
Harvest date	17.7		31.7		19.8		31.7		19.8	
Days between labelling and harvest	0		14		33		0		19	
	a	b	a	b	a	b	a	b	a	b
Leaves	927 $\pm$ 53	74.7	98 $\pm$ 12	7.9	9 $\pm$ 2	0.7	652 $\pm$ 13	69.5	4 $\pm$ 0	0.4
Stem	271 $\pm$ 37	21.8	121 $\pm$ 27	9.8	50 $\pm$ 3	4.1	245 $\pm$ 5	26.1	15 $\pm$ 2	1.6
Pods	40 $\pm$ 14	3.2	399 $\pm$ 43	32.1	223 $\pm$ 16	17.9	26 $\pm$ 2	2.8	51 $\pm$ 7	5.5
Seeds	4 $\pm$ 2	0.3	298 $\pm$ 30	24.0	481 $\pm$ 18	38.7	14 $\pm$ 3	1.5	498 $\pm$ 9	53.2
Root	-	-	40 $\pm$ 7	3.2	21 $\pm$ 2	1.7	-	-	20 $\pm$ 3	2.2
Total	1242 $\pm$ 95	100	955 $\pm$ 62	76.9	784 $\pm$ 45	63.1	937 $\pm$ 174	100	588 $\pm$ 35	62.9

Sv 0621

Stage IV							Stage V			
Harvest date	15.7		29.7		16.8		29.7		16.8	
Days between labelling and harvest	0		14		32		0		18	
	a	b	a	b	a	b	a	b	a	b
Leaves	736 $\pm$ 83	61.9	119 $\pm$ 21	10.0	13 $\pm$ 3	1.1	557 $\pm$ 52	72.2	30 $\pm$ 8	3.9
Stems	155 $\pm$ 33	13.1	73 $\pm$ 14	6.1	21 $\pm$ 3	1.8	121 $\pm$ 12	15.6	8 $\pm$ 1	1.0
Lateral ²⁾ branches	248 $\pm$ 30	20.8	52 $\pm$ 45	4.4	22 $\pm$ 18	1.9	70 $\pm$ 42	9.0	70 $\pm$ 31	9.0
Pods	42 $\pm$ 3	3.5	251 $\pm$ 1	21.1	168 $\pm$ 33	14.1	21 $\pm$ 4	2.7	30 $\pm$ 3	3.9
Seeds	8 $\pm$ 2	0.7	390 $\pm$ 41	32.8	424 $\pm$ 40	35.6	4 $\pm$ 2	0.5	484 $\pm$ 27	62.7
Root	-	-	19 $\pm$ 4	1.6	6 $\pm$ 1	0.5	-	-	9 $\pm$ 1	1.1
Total	1189 $\pm$ 139	100	904 $\pm$ 164	76.0	653 $\pm$ 41	54.9	772 $\pm$ 92	100	630 $\pm$ 31	81.6

1) Plants decapitated on 3rd July

2) All branches except the two that were treated together as the main shoot.

determine if it is the increased vegetative growth that affected pod development or vice versa. Competition between vegetative and reproductive growth is well documented (Hodgson and Blackman 1957, Ryle 1970 and McEwen 1973).

A comparison between *Primus* and *Skladia* shows some differences as to how the photosynthate is distributed in the plant. Thus *Skladia* had a 24% smaller top zone (in dry matter) and this resulted in a decreased ^{14}C assimilation with 18% as compared to *Primus* (calculated by graphic representation). However, lower losses (41% against 47%) and a higher percentage of assimilates which were translocated to the seeds (65% against 60%) compensated for the decreased assimilation in *Skladia*. Similar differences between varieties have also been reported in *Phaseolus vulgaris* (Peet et al. 1977).

Even if the vegetative top growth has some negative influence on reproductive growth, it is obvious that the uppermost leaves supply the seeds with much of the plant photosynthates that are needed. An estimate using recovered ^{14}C , one hour after treatment, to calculate totally assimilated carbon, shows that 38% and 34% was fixed by the top zone in *Primus* and *Skladia*, respectively. During this period newly assimilated carbon dominates. Only 10% of the ^{14}C recovered in the seeds at maturity was fixed before pod growth. Thus the top zone must play an important role as a source for assimilate during pod filling.

A ten per cent re-translocation to seeds of photosynthates fixed before pod growth is comparable with that reported in soybean by Hume and Criswell (1973). In pea this figure was only 2%, but that of early fed ^{15}N was as high as 51% (Pate and Flinn 1973). This high recovery percentage of ^{15}N fixed prior to flowering was also found in field beans (Cooper et al. 1976), although in the field beans total re-distributed nitrogen to seeds was much less than in peas. Thus even in the case of nitrogen, the plant has to rely to a great extent upon nitrogen fixed during reproductive growth. However, as Cooper et al. suggested, even if redistribution only makes a small contribution, qualitatively it could be much more important.

In the utilization of photosynthates decapitated *Skladia* and Sv 0621 showed some differences. Decapitated *Skladia* plants assimilated about 11% more ^{14}C than Sv 0621, but only half of this surplus was translocated to the seeds. Furthermore, 33 and 35% of initial assimilated ^{14}C was recovered in the seeds, whereas 43 and 41% was lost at maturity in decapitated *Skladia* and Sv 0621, respectively.

The two phase pattern of early fixed ^{14}C -labelled assimilate losses is similar to that reported by Ryle et al. (1976) in young barley and maize plants. According to their results phase 1 is completed within 24 h. The main losses are from those respiratory processes associated with biochemical pathways through which assimilate is transformed into plant biomass and thus could be called synthetic respiration (R_s). In an energy analysis of the biochemical pathways, Penning de Vries (1975) calculated R_s to be 25-30 per cent. This is consistent with the phase 1 losses reported in this study.

Phase 2 losses of ^{14}C -labelled assimilates originate from respiratory effluxes due to protein turnover and maintenance of ion concentrations and other aspects of cellular integrity (Ryle et al. 1976). This type of respiration is commonly called maintenance respiration (R_m). The range of $0.5-0.7\% \text{ day}^{-1}$ of maintenance respiration in this study compares favourably with that quoted by Penning de Vries (1975).

Assimilate fixed during seed filling periods (stage IV-VI) was subjected to an increasing average respiratory rate ranging from 1.2% day⁻¹ at stage IV to 3.1% day⁻¹ at stage VI, compared with an average rate of 0.7-1.0% day⁻¹ at stages I-III. The increased losses are to be expected. Assimilates at reproductive stages are subjected to higher translocation and re-translocation activities as well as to new synthesis in the seeds. These are energy-requiring processes affecting respiration rate.

Assimilate fixed during stage IV-VI and to a certain degree also during stage III was first translocated to the pods and from there to the seeds. This could explain the changed pattern in respiratory losses. By comparing IV and V it is possible to correlate the trend of respiratory losses with that of assimilate distribution. In stage IV there is a successive translocation of assimilates to seeds, but in stage V the translocation to seeds is almost completed within seven days.

The main purpose of the study of decapitated *Skladia* and Sv 0621 was to gain further information regarding possible differences in their assimilation and distribution patterns. However, since intact *Skladia* plants at stages IV and V showed similar dry matter accumulation as in 1973, some comparisons have also been made between intact and decapitated plants. Thus recovered activities in 1973 have been multiplied by 0.83 to compensate for the lower specific activity in 1975. The factor of 0.83 is calculated from the differences in ¹⁴C assimilation per mg leaves in 1973 and 1975. Because of this uncertainty only different trends should be compared, since a comparison of absolute values of ¹⁴C assimilation in 1973 and 1975 can be made only with the assumption that there were no differences in assimilation intensities.

Figure 2.4a shows accumulated ¹⁴C in whole plants and in pods. The only difference is the lower amount of ¹⁴C accumulated in plants of Sv 0621, mainly as a result of lower accumulation in vegetative parts. Accumulation in pods and seeds followed almost the same trend in both decapitated and normal plants as well as in Sv 0621.

Analysis of accumulated activity in individual plant parts shows only small differences in the pattern of ¹⁴C accumulation in pods and seeds (Figs. 2.4 b-d). When comparing vegetative plant parts, the stems show similar accumulation patterns although total activity differs. When comparing the leaves, both decapitated *Skladia* and Sv 0621 show a maximum at the time of early seed growth, while intact *Skladia* does not. If, however, the ¹⁴C accumulated in the top zone is added to the leaf values, they appear quite similar to those of decapitated *Skladia*. In other words, the normal contribution of assimilates from upper leaves is in decapitated plants compensated by an increased assimilation by the lower leaves. In Sv 0621 lateral branches also contributed assimilates and consequently their activity should be added to the leaf and stem values. The accumulation patterns of decapitated *Skladia* and Sv 0621 are then quite similar.

One difference that remains is the increased accumulation of ¹⁴C in roots of decapitated *Skladia* as compared to that of Sv 0621. This might be explained by the development of lateral branches in Sv 0621. According to Leonard (see 1.4.3) root growth is negatively influenced by development of lateral branches.

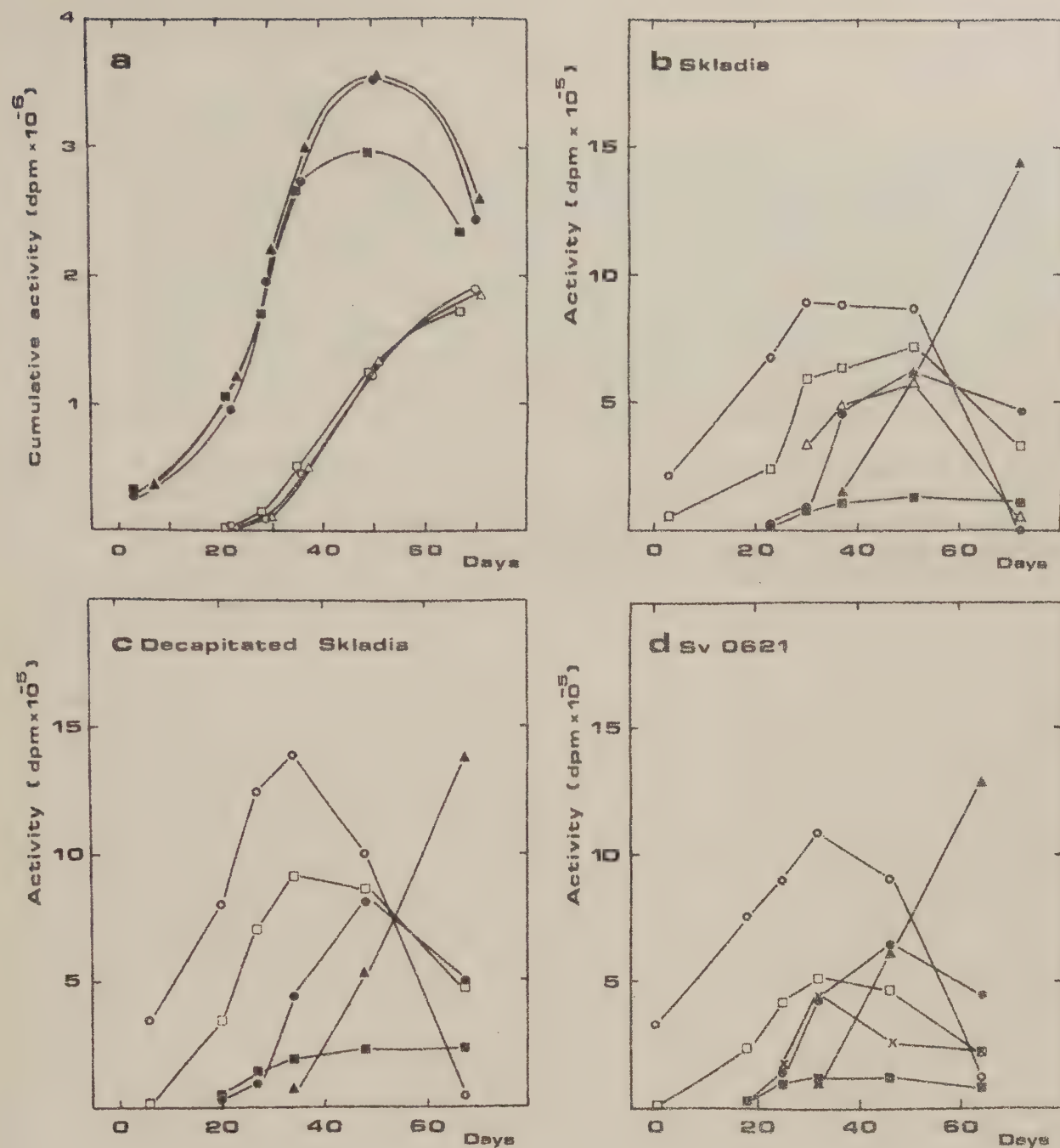


Fig. 2.4 a Accumulated ^{14}C in pods (open symbols) and in whole plant (closed symbols).
 ● Skladia. ▲ Decapitated Skladia and ■ Sv 0621.
 Values for Skladia from 1973 and decapitated Skladia and Sv 0621 from 1975. Further details in the text.

Fig 2.4 b-d Accumulated ^{14}C in individual plant parts from initial flowering to maturity.
 ● Leaves. □ Stem. △ Top. ● Pods.
 ▲ Seeds. ■ Roots. X Lateral branches.

2.6 Conclusions

The growth of the plant is accompanied by a shift of the photosynthetic "center" towards newly developed leaves. Therefore, the importance of the top zone as a source of assimilates increases at the same time as lower leaves undergo senescence. Normally more than 30% of total assimilated carbon is fixed by the top zone at seed filling stages. The ^{14}C accumulation in pods did not change significantly in the decapitated plants or the mutant. The loss of the top zone was compensated for, firstly by an increased assimilation rate in the lower leaves of these plants as well as in the leaves and lateral branches of Sv 0621, and secondly by the fact that the assimilates became more effectively used.

A comparison between the patterns of assimilate distribution in decapitated Skladia and in Sv 0621 did not show any clear-cut differences assuming the influence of lateral branches is not taken into account. Thus determined growth, either through decapitation or genetic manipulation seems to have similar effects of the assimilation and distribution patterns of assimilates.

CHAPTER III

DISTRIBUTION PATTERN OF ASSIMILATE FROM THE TOP ZONE

3.1 Introduction

In this study ^{14}C assimilation and its distribution from the vegetative top is followed during the six weeks prior to maturity. This period covers the whole maturity cycle during which the vegetative top increases in importance as a source of assimilates (see 2.5).

3.2 Plant material

Primus plants grown outdoors in the summer of 1974 (for further details see 2.2).

3.3 Methods

3.3.1 Experimental design

During the six weeks prior to maturity top zones of four Sklardia plants were labelled with $^{14}\text{CO}_2$ each week. In order to confine labelling to only the top zone, the rest of the plant was covered with black plastic during the labelling. On each treatment day, one plant was harvested 45 min after labelling and the rest were harvested at maturity. At harvesting the plants were divided into leaves, stems, top zones, roots, pods and seeds at the two uppermost nodes (pods A) and other pods and seeds (pods B).

3.3.2 Administration of $^{14}\text{CO}_2$ and radiochemical analysis

(See 2.3.3 and 2.3.3)

3.4 Results and discussion

During the first and second week (46 and 52 days after initial flowering) assimilates were accumulated in the stem (Table 3.1). After that the stem lost weight. This coincided with a rapid increase in pod weight (Fig. 3.1). As the leaves are concerned they lost weight just prior to maturity.

Table 3.2 shows that total top zone photosynthesis reached a maximum 58 days after flowering and that the rate of photosynthesis was at a maximum.

At maturity ^{14}C was recovered in all parts of the plant. During the first three weeks, i.e. at the time of rapid pod growth, more ^{14}C was recovered in the root and stem than during the last three weeks. This shows that there are metabolic activities in the root and stem which are supplied by assimilates in the top zone, although the ^{14}C -activity was relatively low as compared to that in pods. Thus these results confirm the suggestion by Tamaki and Naka (1972) that top leaves play an essential role in maintaining root metabolism.

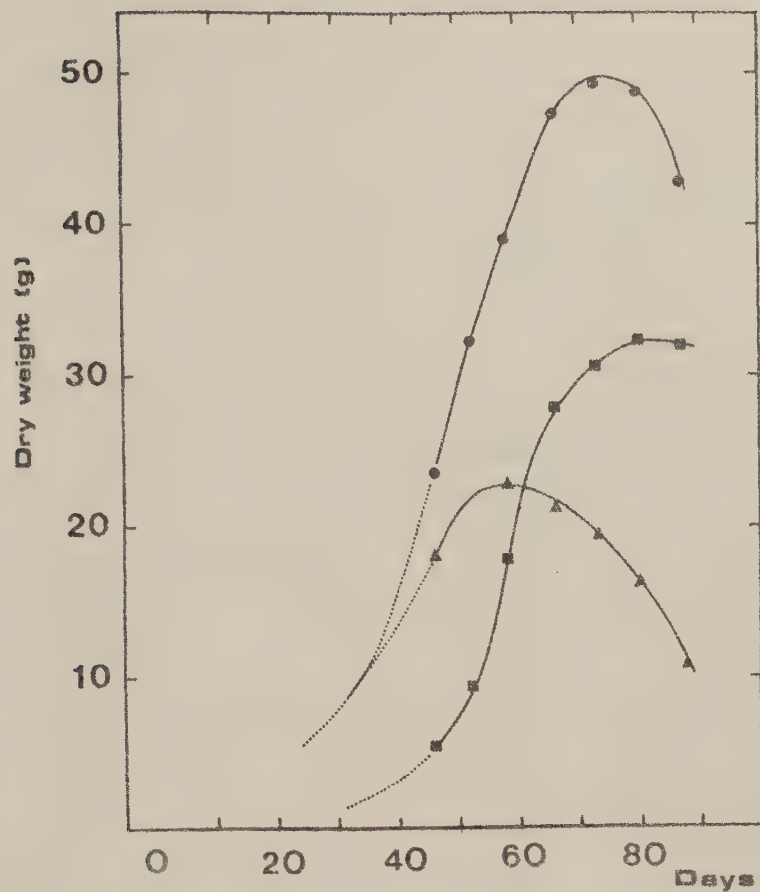


Fig. 3.1. Dry matter accumulation in vegetative and reproductive material from initial flowering until maturity.
 ● Total dry matter. ▲ Vegetative dry matter.
 ■ Reproductive dry matter.

The amount of ^{14}C translocated from the top zone to the two uppermost pod bearing nodes was fairly constant throughout the study. However, relative to total recovered ^{14}C it showed an increase. Recovered ^{14}C in other pods showed an overall decrease. These findings could indicate that the supply of assimilates from top leaves do not limit pod growth, although it is possible that the translocation capacity to the seeds may be limiting.

In this study labelling of whole plants was not conducted, hence it is not possible to compare upper leaf assimilation to whole plant assimilation during the maturity cycle. However, in the experiment reported in chapter 4, whole plants grown at comparable conditions were labelled 43 days after initial flowering. At this stage 46% of the total ^{14}C which was recovered 50 min after labelling, was found in top zones. As shown in chapter 2 lower leaves gradually senesce. Thus the relative contribution of upper leaf assimilation must increase with increasing age.

Table 3.1 Dry weights (g) of various plant parts during the six weeks prior to maturity. The plants were grown outdoors in pots.

Plant part	Days after initial flowering						
	46	52	58	66	73	80	87
Leaves	3.7	7.0	7.1	7.6	7.0	4.9	>10.1
Stem	11.1	12.9	10.6	7.8	8.8	8.5	
Top zone	3.2	3.0	3.5	4.2	2.9	3.0	0.7
Pods A ³⁾	>5.5	>9.4	>17.9	>27.9	>30.7	>32.3	4.2
Pods B ³⁾							27.8
Root	- 1)	-	-	-	-	-	(10.8) ²⁾
Total	23.5	32.2	39.1	47.3	49.4	48.8	42.8

1) Roots were not collected in plants harvested immediately after treatment

2) Root weights not included in total sum

3) Pods A = Pods at the two uppermost pod-bearing nodes
 Pods B = Pods at remaining pod-bearing nodes

Table 3.2. ^{14}C -activity recovered in different plant parts after labelling the top zone at regular intervals during six weeks prior to maturity.

Day of labelling (Days after initial flowering)	Total activity recovered 50 min after treatment (dpm·10 ⁻³)	Photosyn- thetic activity per mg top dry weight (dpm/mg)	Recovered ¹⁴ C-activity in various plant parts at maturity (dpm · 10 ⁻³)							Percentage of total recovered activity in pods (%)			Recovery percentage in whole plants (%)
			Stem	Top zone	Root	Pods			Whole plant	Pods			
						A	B	A+B2)		A	B	A+B	
46	535	167	34	21	17	64	277	341	412	15.5	67.2	82.8	77.0
52	596	199	23	4	9	64	210	274	310	20.6	67.7	88.4	52.0
58	681	194	10	3	12	59	263	322	347	17.0	75.8	92.8	51.0
66	531	126	8	3	4	79	186	265	280	28.2	66.4	94.6	52.7
73	290	100	8	2	7	60	111	171	188	32.0	59.0	91.0	64.8
80	215	72	3	2	3	32	54	86	94	34.9	57.4	92.3	43.7

1) The plants were harvested 87 days after initial flowering

2) Pods A = Pods at the two uppermost pod-bearing nodes
B = Pods at the remaining pod-bearing nodes

CHAPTER IV

INFLUENCE OF PARTIAL DEFOLIATION OF DIFFERENT ZONES ON CARBON ASSIMILATION AND DISTRIBUTION PATTERNS

4.1 Introduction

Carbon assimilation is not only influenced by environmental factors such as light, temperature, water and CO_2 , but also by internal factors such as protein- and chlorophyll contents. These are changing throughout the plant ontogeny and thus photosynthesis is to a great extent controlled by these factors (see 1.4.1). Through various manipulations it is also possible to influence the internal factors and thus photosynthesis.

Defoliation for example may delay senescence of the remaining leaves (Maggs 1964, Woolhouse 1974, Hodgkinson 1974) and increase their photosynthetic activity (Woolhouse 1974, Callow and Woolhouse 1973, Meidner 1970). It may also influence symbiotic nitrogen fixation (Lawn and Brun 1973) as well as decrease the pool of nitrogen available for retranslocation (Sinclair and de Wit 1976) and thus indirectly affect photosynthesis.

Defoliation also changes distribution of carbon assimilates. Defoliation between the source leaf and the root increases the amount of assimilates translocated to the root (Thrower 1962), whereas more ^{14}C is recovered in the apex if defoliation is carried out between the source leaf and the apex (Thaine et al. 1959).

The present study was conducted to glean information about the effects of partial defoliation on the assimilation and distribution patterns of carbon in field beans.

4.2 Plant material

Plants of the variety Primus were used from the same pool as described in 2.2 and 3.2.

4.3 Methods

4.3.1 Experimental design

The effects of partial defoliation of three different zones on assimilation and distribution patterns were studied by labelling with $^{14}\text{CO}_2$. Defoliation and labelling were conducted in 1973 and 1974 according to Table 4.1.

The plants were divided into three zones. Zone A - the lower part up to the first flowering node (about six nodes), zone B - the middle region with all flowering nodes (about ten nodes) and zone C - the vegetative top zone (about five nodes). All combinations of partial defoliation were tested. In other words, Exp. I, included four different combinations of defoliation and Experiments II and III eight combinations. In Experiments I and III defoliation was carried out immediately prior to labelling with $^{14}\text{CO}_2$, and in Exp. II it was done about three weeks before labelling. Experiments II and III were repeated in 1974 but Exp. I was not. Three plants from each combination of defoliation were treated. In 1974 a fourth plant was also labelled and this was harvested

45 min after labelling. The other plants were harvested on 30th July in 1973 and on 10th August 1974.

Table 4.1 Day of defoliation and labelling of Experiments I-III in 1973 and 1974.

Exp. no.	Year	Day ¹⁾ of defoliation	Day of labelling	Development stage at time of defoliation
I	1973	early 22	early 22	Zone A and zone B developed.
II	1973	early 22	late 41	As in I (The leaves were pinched off as they grow out on plants were zone C should be missing.
	1974	18	43	
III	1973	late 41	late 41	Zone A, zone B and zone C developed. Rapid pod filling.
	1974	43	43	

1) Days after initial flowering

4.3.2 Administration of $^{14}\text{CO}_2$ and radiochemical analysis

For administration of $^{14}\text{CO}_2$ see 2.3.2 and for radiochemical analysis see 2.3.3.

4.4 Results

In 1974 total dry weight per plant was increased by about 40% as compared with that in 1973 (compare Figs. 2.1a and 3.1). Table 4.2 shows pod dry matter two weeks before maturity. In Experiments I and II defoliation was carried out at the same time and in Exp. III, about three weeks later. This affected pod weight which was higher in late defoliated plants. Compared to late defoliation the plants responded particularly negatively to early defoliation of zone B. Where zone B was intact, effects on pod weights were small and in 1974 the combination AB- (zone C missing) showed a positive effect.

Comparisons between different combinations of defoliations show that zone B plays the most important role and that zone C could be excluded without serious consequences. In 1973 several combinations of defoliation resulted in an increased pod yield. However, according to the reproductive growth curve (Fig. 2.1a), pod yield in intact plants should at this point be about 15 g. Thus it is possible that the intact plants diverge from the population average.

In 1974 total dry weight of the top zone leaves was doubled as compared with that in 1973, while no significant differences were observed in the other two zones (Table 4.3).

Table 4.2 Pod dry weights (g) from plants defoliated at two different occasions according to Table 4.1,

Year	Exp. no.	ABC	-BC ¹⁾	A-C	AB-	A--	-B-	--C	---
1 9	I ²⁾	13.2 ± 1.4	12.7 ± 1.5	7.6 ± 1.4	-	-	-	4.1 ± 1.2	-
7 3	II		13.5 ± 0.5	7.8 ± 0.7	14.3 ± 0.7	4.7 ± 1.1	13.9 ± 1.5	5.5 ± 0.6	1.4 ± 0.4
	III	13.2 ± 0.2	15.6 ± 1.4	13.5 ± 0.5	16.2 ± 0.3	9.7 ± 0.4	15.8 ± 1.1	14.7 ± 0.9	11.4 ± 1.1
1 9	II		15.1 ± 1.7	13.1 ± 0.9	18.8 ± 0.6	3.6 ± 0.6	13.2 ± 0.5	9.4 ± 2.4	1.1 ± 0.1
7 4	III	19.6 ± 1.6	17.2 ± 0.5	16.3 ± 1.6	15.9 ± 1.4	9.2 ± 1.4	13.9 ± 0.2	14.1 ± 2.3	7.8 ± 1.9

1) - indicates a missing zone.

2) See Table 4.1. 3) Mean $\pm$ S.E.; n = 3.

Table 4.3 Mean leaf dry weights at harvesting (g)

Year	Zone ¹⁾		
	A	B	C
1973	1.01 $\pm$ 0.09 ²⁾	3.33 $\pm$ 0.22	1.55 $\pm$ 0.10
1974	0.83 $\pm$ 0.11	3.91 $\pm$ 0.25	3.07 $\pm$ 0.31

1) See Table 4.1.

2) Mean $\pm$ S.E.; n = 3.

Table 4.4 shows that the photosynthetic activity expressed as assimilated ^{14}C per mg dry matter of leaves varied after defoliation. In intact plants top leaves (zone C) showed the highest assimilation rate and lower leaves (zone A), the lowest. When the leaves of one zone was missing, the leaves of zone A reacted with an increased assimilation rate. Zone B leaves showed a similar reaction, whereas those of zone C did not.

Table 4.4 Influence of partial defoliation of different zones on leaf photosynthesis (dpm mg^{-1} leaf d.m.)

	Combination of defoliation ¹⁾						
	ABC	AB-	A-C	-BC	A--	-B-	--C
A	54	143	129	---	66	---	---
B	143	163	---	172	---	178	---
C	185	---	187	186	---	---	171

¹⁾ see Table 4.1

Fig. 4.1 shows recovered ^{14}C -activities in various plant organs. In Exp. I intact plants showed the highest recovered ^{14}C , whereas plants that were totally defoliated showed the lowest. Furthermore, loss of leaves of zone B reduced recovered ^{14}C four times as much as compared with that of zone A. Relatively, recovered ^{14}C in pods decreased with increasing defoliation but otherwise there were no main differences in the pattern of assimilate distribution (Table 4.5).

In plants labelled three weeks after Exp. I and defoliated prior to labelling (Exp. III), total recovered ^{14}C was lower as compared to corresponding defoliations in Exp. I. If, however, defoliation was carried out three weeks before labelling (Exp. II), total recovered ^{14}C was increased as compared to that in corresponding defoliation in Exp. I.

In Exp. III, as in Exp. I, the loss of zone B was more serious than that of zone A. The pattern of assimilate distribution was quite different from that in Exp. I. Labelling in Exp. III was carried out during rapid pod growth and hence most of the ^{14}C was recovered in pods, whereas in Exp. I the stem and leaves were still growing and assimilates had accumulated.

At the time of labelling in Experiments II and III, the top zone was also developed, and thus the number of combinations were doubled. When zone A was defoliated, either at an early or late stage, the distribution of assimilated ^{14}C during the pod filling stage was not affected (expressed as a percentage of total recovered ^{14}C). However, total recovered ^{14}C was lower especially for early defoliated plants in 1974.

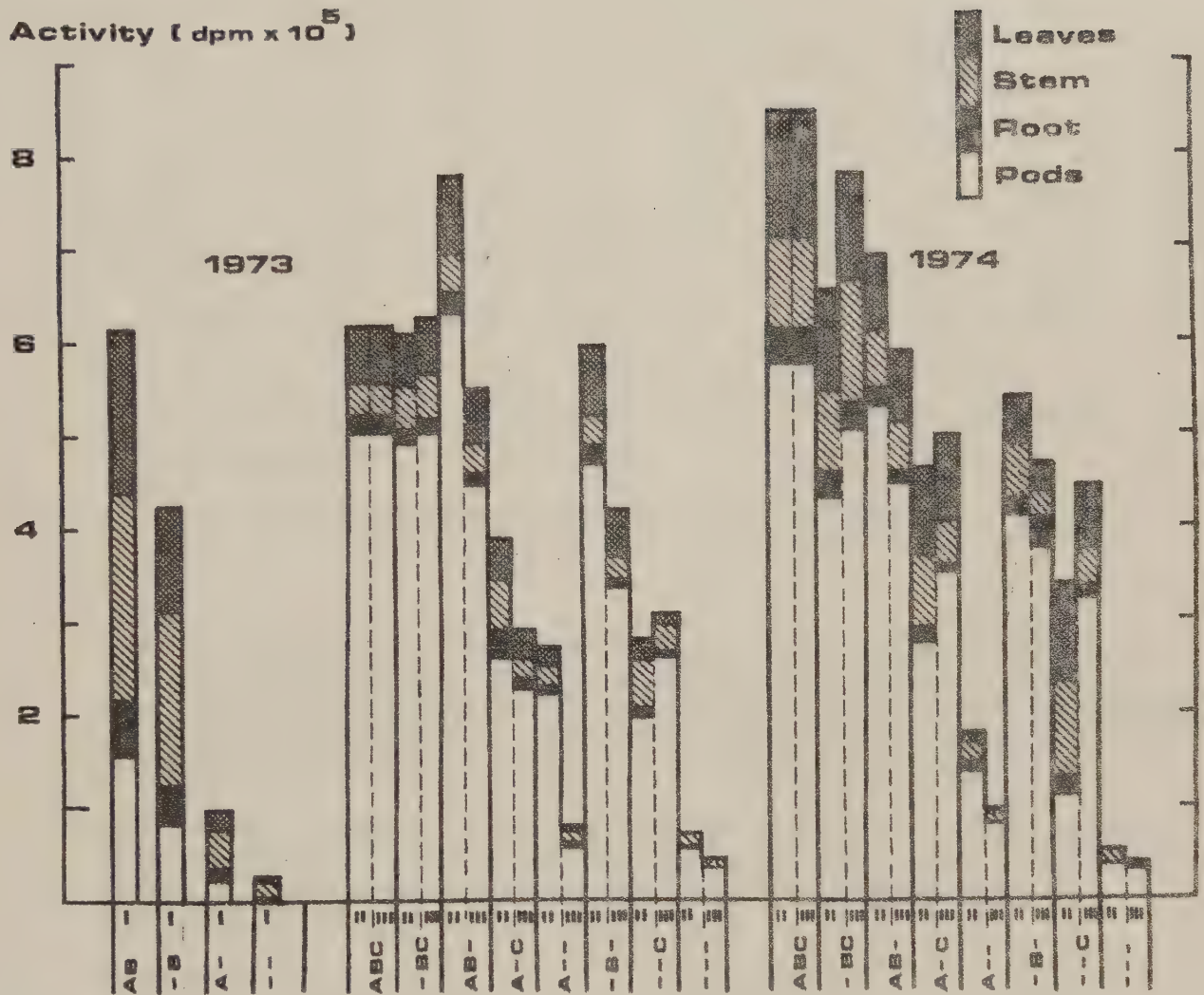


Fig. 4.1 ^{14}C recovered in various plant organs after different combinations of defoliation and time between defoliation and labelling. The plant is divided into three zones. A = lower leaves, B = mid-region leaves and C = upper leaves. Defoliated zones are indicated with -. Experiment I = early defoliation, early labelling; Experiment II = early defoliation, late labelling and Experiment III = late defoliation, late labelling.

Table 4.5 Recovered ^{14}C in pods in percentage of total recovered ^{14}C (%)

		Combination of defoliation ¹⁾						
		ABC	AB-	A-C	-BC	A--	-B-	--C
	Exp I	-2)	23+2	---	---	21+2	20+3	---
1	Exp II	81+1	81+2	68+3	79+2	82+1	78+1	69+5
9	Exp III	81+1	81+2	78+2	76+2	69+5	81+1	85+1
7	Exp II	67+3	77+4	60+3	65+5	78+4	76+3	33+8
3	Exp III	67+3	76+2	71+2	65+1	85+3	80+1	72+4
1								
9								
7								
4								

1) see Table 4.1

2) Zone C was not developed when Exp I was labelled.

When zone B was defoliated, total recovered activity was decreased to about half that of intact plants. In 1973 early defoliation had a positive effect on recovered ^{14}C as compared to that in late defoliation. In 1974 it was reversed. In both years a larger proportion of the total recovered ^{14}C was found in pods of late defoliated plants.

Defoliation of zone C, on the other hand, resulted in a reduction of total recovered ^{14}C . Early defoliation in 1973 also showed a positive effect as compared with that in intact plants. The proportion of recovered ^{14}C in pods was not different.

If all but zone A was defoliated, total recovered ^{14}C was low. Early defoliation showed, however, a strong positive effect as compared with that during late defoliation.

When only zone B was defoliated, especially in early defoliated plants from 1973, a small reduction in the recovered ^{14}C occurred. There was no significant influence on the distribution pattern of ^{14}C assimilates.

Zone C showed an intermediate position between zone A and zone B. Early defoliation resulted in less ^{14}C being recovered as compared to that during late defoliation. The proportion of recovered ^{14}C in pods was decreased in early defoliated plants.

Figure 4.2 shows the differences in total recovered ^{14}C between Experiments II and III. In 1973 pre-defoliation increased the total recovered ^{14}C as compared to that in plants that were defoliated prior to labelling in all but two of the combinations. In 1974 the differences were decreased in combinations that were lacking zone C. For combinations with zone C present, the negative influence of early defoliation was even higher than in 1973. Differences of recovered ^{14}C in Exp. II are about 90×10^3 dpm lower than the differences in 1973.

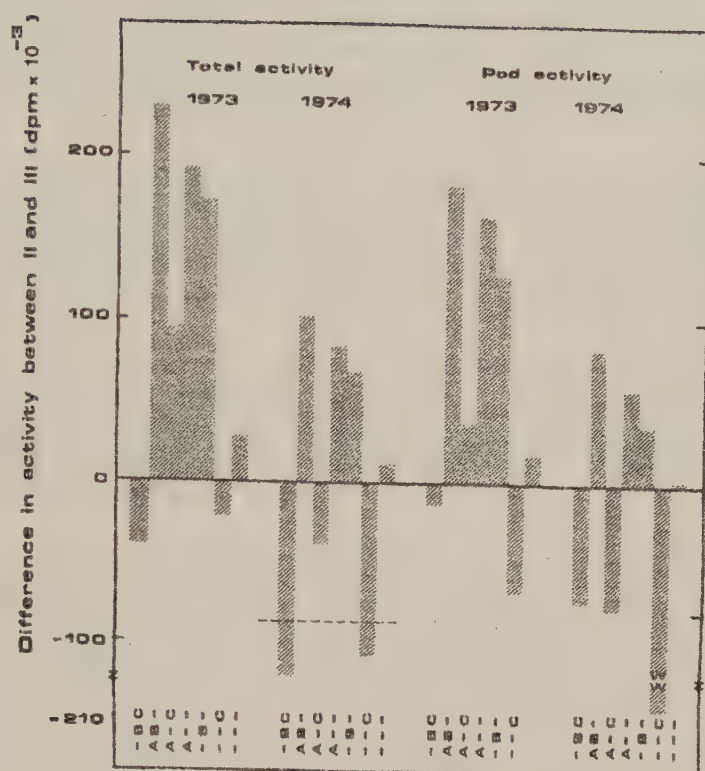


Fig. 4.2 Differences in total recovered ^{14}C between Experiments II and III during 1973 and 1974. For further details see Fig. 4.1.

4.5 Discussion

In Exp. III (defoliation immediately before labelling) the increased ^{14}C assimilation in the lower leaves (with upper leaves missing), is probably mainly a result of reduced mutual shading. The time period between defoliation and labelling was less than 30 min and new synthesis or activation of proteins necessary for increased assimilation could hardly have occurred to any great extent.

In Exp. II, on the other hand, the time period between defoliation and labelling was three weeks and thus adaptation could have occurred. All combinations where zone C was defoliated showed higher recovered ^{14}C values than those of comparable combinations of late defoliation. This implies that lower leaves could increase their assimilation, but that the upper leaves could not, since they already were assimilating at a high level. The mechanism behind this is not quite clear.

One possible explanation may involve an adaptation to the increased light intensities after removal of the upper leaves. This adaptive potential is greatest during leaf expansion (Jurik et al. 1979), although fully expanded leaves also retain some capacity to adapt to altered light regimes (Bunce et al. 1977). Leaves transferred from one light regime to another show anatomical changes with regard to leaf thickness, mesophyll surface area, and specific leaf weight, as well as physiological and biochemical changes concerning chlorophyll contents, photosynthetic unit sizes and densities, total proteins, RuBPCase activity, glycolate oxidase activity, and malate dehydrogenase activity (Bowes et al. 1972, Bunce et al. 1977, and Jurik et al. 1979).

In soybean leaves, however, increased light (from 250 to 850 $\mu\text{E m}^{-2} \text{s}^{-1}$) resulted in decreased net photosynthesis as a result of increased photorespiration (Bunce et al. 1977). However, the adaptation was only followed during the six days, and it is possible that the adaptation process to high photorespiration rates require more than six days.

Responses similar to those caused by light adaptation have also been observed after manipulations with the sink-source relationship. The demand for assimilate is believed to influence the leaf either through a feed-back mechanism (Neales and Incoll 1968) or through growth regulators (Wardlaw 1968).

There were only small differences in the distribution pattern of ^{14}C to the pods. In early defoliation of zone A and/or zone B a lower percentage of ^{14}C was recovered in the pods, probably because of too low a number of pods. Late defoliation, however, did not affect pod set as did the early defoliation, since ^{14}C was translocated to pods to a similar extent in all combinations of defoliation. This is interesting since studies in soybeans (Belikov 1955), peas (Linck and Sudia 1962, Harvey 1973), and field beans (Ishag 1973b) suggest a close relation between the leaf and its subtending pods.

The experiment is in line with McEwen's finding (1972) that the leaves of zone B play a dominating role as a source of assimilates. It has also been shown that the leaves of zone A play an important role at pod set and that zone C, depending on its size, can be compensated for by increased assimilation in lower leaves. The compensation ability was highest for leaves of zone A and lowest for those of zone C.

CHAPTER V

THE INFLUENCE OF INDETERMINATE AND DETERMINATE GROWTH HABIT ON DIFFERENT CHARACTERISTICS DURING THE ONTOGENESIS OF A PLANT

5.1 Introduction

The ability to increase net photosynthesis (P_N) with different treatments such as decapitation, debudding and debranching have been reported for several crops. For example partial defoliation of beans (*Phaseolus vulgaris* L.) resulted in an increase in P_N , RuBPCase activity (Wareing et al. 1968), and stomatal conductance (Meidner 1970). In lucerne (*Medicago sativa* L.) partial defoliation induced rejuvenation of senescent leaves (Hodgkinson 1974), and similar effects have been reported for debranched grasses (*Lolium multiflorum* L.) (Gifford and Marshall 1972), and decapitated *Perilla* (Callow and Woolhouse 1973).

Responses similar to those after decapitation have been obtained by spraying the leaf with kinetin (Richmond and Lang 1957, Wareing et al. 1968, Treharne et al. 1970, Dyer and Osborn 1971, and Adedipe et al. 1971), gibberellin (Treharne et al. 1970), and auxin (Turner and Bidwell 1965).

The results of the study with partially defoliated plants (Chapter 4) showed that P_N was positively influenced by the partial defoliation. In the present study the effects of decapitation on P_N and other leaf characteristics have been investigated. Parallel studies have also been carried out in Sv 0621 to ascertain whether the mutant reacted in a similar way as the decapitated plants.

5.2 Materials and Methods

5.2.1 Plant materials

In the study the commercial variety Primus (Svalöv) with indeterminate growth habit, and the mutant Sv 0621 (Sjödin 1971) with determinate growth habit were used. The plants were cultivated under controlled conditions in a growth chamber, in 1.5 l clay pots with one plant in each. The potting mixture consisting of 2/3 medium heavy soil and 1/3 of peatmoss, was mixed with 1 g of a compound mineral fertilizer ("Blåkorn"). Every three weeks 50 ml of a solution containing 5 g KH_2PO_4 and 5 g K_2SO_4 per litre were added to each of the pots. The pots were watered daily.

During the first seven weeks the plants were exposed to 16 h of light at an irradiance of 150 Wm^{-2} , and to a temperature of 12°C in light and 8°C in darkness. The relative humidity was 70% during the light period and 95% during the dark period. At the beginning of the 8th weeks the temperature was raised to 18°C in light and 14°C in darkness.

5.2.2 Plant treatment

Variations in the rate of photosynthesis (P_N), diffusion resistances, specific leaf weight, protein, chlorophyll and carbohydrate contents were studied during the ontogeny of five different groups of plants.

a) Control plants b) decapitated plants with laterals c) decapitated plants without laterals d) Sv 0621 with laterals and e) Sv 0621 without laterals.

The measurements were started when the normal plant had ten to twelve flowering nodes and 18 nodes in total. By this time all leaves of Sv 0621 were developed on the main stem. The measurements were done on one of the two outermost leaflets of leaf number 15 on indeterminate plants and on number 8 of the mutants. Twelve days later 2/3 of the normal plants were decapitated at the 18th node and as branches grew out they were pinched off on half of the decapitated plants and half of the mutants. At the time of decapitation leaf 15 had reached its maximum leaf area.

5.2.3 Gas exchange measurements

P_N was measured with a set-up similar in basic design to that of Gastra (1959). Transpiration was measured simultaneously with a differential psychrometer (Bierhuizen and Slatyer 1964a). The infra-red analyzer (URAS II) was calibrated against two known gas mixtures, 342 $\mu\text{l/l}$ and 282 $\mu\text{l/l}$ and the psychrometer against a hygrophil (Ultrakust). The whole apparatus was placed in a growth chamber with a temperature of 20°C and a R.H. of 60%.

The leaf cuvette was made of aluminium with a glass cover. In the walls channels were drilled, through which tempered water was circulated for temperature control. A fan placed in the cuvette circulated the air to reduce gradients of CO_2 and H_2O , and reduce the boundary layer resistance. Leaf temperature was measured with a plastic-shielded bead-thermistor (Hafö 2.0 k Ω , Stockholm) gently pressed against the lower side of the leaf.

The illumination system consisted of a halogen metal vapour lamp (HQI-TS 400 W Osram), a neutral filter, a heat absorbing filter and a 10 cm running water filter. Irradiance was measured with a miniature silicon solar cell (Hoffman photovoltaic detector capsule, type E.A7), calibrated against a Kipp & Zonen Solarimeter. Total irradiance at the leaf surface was kept constant at 280 Wm^{-2} and photosynthetic active radiation PhAR was kept at 260 Wm^{-2} .

Leaf temperature was kept at $20.0 \pm 0.1^\circ\text{C}$ and R.H. at approximately 65%. The leaflet, still attached to the plant was gently sealed into the cuvette and after 5-20 min steady state gas-exchange conditions occurred. Flow rate was adjusted so that CO_2 depletion across the cuvette was between 15-25 $\mu\text{l/l}$. The ambient CO_2 concentration was maintained at $324 \pm 5 \mu\text{l} \cdot \text{l}^{-1}$. Leaf area was estimated by measuring a replica made of green paper in a photoelectric planimeter.

Calculations of P_N were made according to equation 1 (Čatský et al. 1971).

$$P_N = \frac{\Delta\text{CO}_2}{A} \times \frac{J \times 44}{22414} \times \frac{273}{T} \times \frac{P}{760} \quad (1)$$

P_N = rate of net photosynthesis ($\text{mg dm}^{-2} \text{h}^{-1}$)

ΔCO_2 = the difference in CO_2 concentration of the air stream before and after the chamber ($\mu\text{l} \cdot \text{l}^{-1}$)

J = air flow rate through the cuvette ($l\ h^{-1}$)

A = leaf area (one surface) (cm^2)

T = temperature at which the flowmeters were calibrated and also the temperature at the time of observation (constant at 293 K)

P = barometric pressure (mmHg) at the time of observation, the calibration of the flowmeter having been corrected to 760 mm Hg.

Calculations of transpiration E were made according to equation 2.

$$E = \frac{\Delta e}{A} \times J \times C_T \quad (2)$$

E = rate of transpiration ($g\ dm^{-2}h^{-1}$)

Δe = the difference in water vapour pressure before and after the cuvette (mmHg)

A and J see equation 1.

C_T = factor for converting from vapour pressure to water vapour concentrations

$$(C_T = \frac{273}{T} \times \frac{0.804}{P}) (g\ dm^{-3}\ mmHg^{-1})$$

Calculations of diffusion resistances according to equation 3, 4, 5 and 6 (see Jarvis 1971).

$$(r_a + r_s)_{H_2O} = \frac{(H_2O)_{int} - (H_2O)_a \times 0.36}{E} \quad (3) \quad (\text{Gaastra 1959})$$

$(r_a + r_s)_{H_2O}$ = boundary layer resistance and stomatal resistance for diffusion of H_2O ($s\ cm^{-1}$)

$(H_2O)_{int}$ = saturated water vapour concentration at the liquid-air interface ($g\ m^{-3}$)

$(H_2O)_a$ = water concentration in the ambient air ($g\ m^{-2}$)

E = transpiration rate ($g\ dm^{-2}h^{-1}$)

r_{aH_2O} was taken as the resistance of H_2O evaporation from a water-saturated replica of the leaf, made of green filter paper (Gaastra 1959).

Estimation of r_{aCO_2} and r_{sCO_2} was made according to the relations

$r_{aH_2O} = 1.35 \cdot r_{aCO_2}$ and $r_{sH_2O} = 1.56 \cdot r_{sCO_2}$ (Gale and Poljakoff-Mayber 1968).

Calculations of total resistance to CO_2 in the leaf was made according to equation 4.

$$\Sigma r = \frac{(\text{CO}_2)_a - (\text{CO}_2)_{chl}}{P_N} \times \eta_{\text{CO}_2} \times 0.36 \quad (4)$$

$(\text{CO}_2)_a$ = ambient $[\text{CO}_2]$ in the cuvette ($\mu\text{l}\cdot\text{l}^{-1}$)

$(\text{CO}_2)_{chl}$ = $[\text{CO}_2]$ at the chloroplasts, approximated to be similar to the compensation point τ ($\mu\text{l}\cdot\text{l}^{-1}$).

τ was estimated through extrapolation of a response curve on P_N of varying CO_2 concentrations (Bierhuizen and Slatyer 1964b). τ was treated as a constant throughout the study, although it shows small variations with age (Rawson and Woodward 1976).

P_N = rate of net photosynthesis ($\text{mg dm}^{-2}\text{h}^{-1}$)

η_{CO_2} = density of CO_2 at 20°C and 760 mm Hg = 1.842 mg cm^{-2}

Σr = the sum of all diffusion resistances ($\text{s}\cdot\text{cm}^{-1}$).

Calculations of mesophyll resistances and carboxylating resistances ($r_m + r_x$) were made according to equation 5.

$$r_m + r_x = \Sigma r - (r_a + r_s)_{\text{CO}_2} \quad (\text{s} \cdot \text{cm}^{-1}) \quad (5)$$

In equation 3 the water vapour is assumed to be saturated at the liquid-air interface. There is, however, evidence that the water potential or vapour pressure at the liquid-air interface is reduced. One probable explanation of this could be the presence of an hydraulic resistance (Jarvis and Slatyer 1970). This resistance is in this case included in the stomatal resistance. Since it has no counterpart in the CO_2 transfer pathway, the deviation of stomatal resistance to CO_2 diffusion from the vapour transfer resistance yields an overestimate, and hence an underestimate of the mesophyll resistance, when the mesophyll resistance is estimated as a residual resistance according to equation 5 (Jarvis 1971).

The mesophyll resistance, when estimated as a residual resistance, contains components of CO_2 absorption, and both diffusive and mass transfer components, as well as components which are attributable to carboxylation and photochemical reactions. At saturating irradiance, however, the influence of photochemical reactions is eliminated (Jarvis 1971). Since a saturating irradiance was used in this study the residual resistance was thought as the sum of the mesophyll and carboxylating resistances. Here it is important to notice that the carboxylating resistance is not a diffusion resistance and thus it is not possible to predict quantitatively what effect a change in resistance elsewhere will have upon the rate of the overall process. At best this serves to demonstrate relative magnitudes at any time (Jarvis 1971).

5.2.4 Protein, chlorophyll and RuBPCase

Six discs from leaves taken at the 14th, 15th, and 16th node on three plants from each treatment were punched out and extracts were prepared by homogenizing the pre-weighted leaf samples. The proteins were precipitated by trichloroacetic acid (Björkman 1968a).

Determination of the soluble proteins was based on a modification of the Lowrey method (Hartree 1972). The protein was expressed in equivalents of albumin from Bovine serum (Sigma).

Total chlorophyll concentration was determined in a few ml of the homogenate after extraction with acetone according to the Mackinney-Arnon method (Arnon 1949).

On two different occasions RuBPCase activity was assayed according to Björkman (1968a). The assay was made at 20°C and pH 8.0. The concentration of the whole-leaf homogenate was adjusted so that the reaction was linear for at least three minutes (RuBP-Ba₂ from Sigma and NaH¹⁴CO₃ 0.1 mCi/mmol from Radiochemical Centre, Amersham, England).

5.2.5 Carbohydrates

Leaflets from the 14th, 15th and 16th node were collected between 9.30 and 10.00 (about 5 hours after the dark period). To reduce the effects of undesired defoliation, samples from three nodes of six different plants were used in each determination.

The extraction of ethanol soluble carbohydrates was made according to the methods of Upmeyer and Koller (1973). The ethanol insoluble carbohydrates were, after hydrolysis in 10 ml 1 M H₂SO₄ for 10 min at 100°C extracted as previously described.

The carbohydrate content in the two fractions was determined by the anthrone method according to Loewus (1952). Two solutions of glucose were used as standards (15 and 30 µl/ml). The results are expressed in equivalents of glucose.

5.3 Results

5.3.1 Effects of decapitation on plant development

The conditions in the growth chamber were favourable for vegetative growth. This influenced pod-set negatively. To increase the likelihood of fertilization the flowers were gently squeezed. However, despite this some plants failed to set pods, probably because of self-incompatibility. Such plants continued to grow and set new flowers but without any pod-set. Other plants set one or two pods per node but pod-set was low (Table 5.1).

One effective way to increase pod-set was decapitation together with debudding. This doubled the average number of pods per node, and on some plants up to nine pods were set. However, the stimulative effect of decapitation was reduced by the development of lateral branches. The number of pods per plant was lower because of the lower number of nodes with pods as compared with control plants. On the other hand,

Table 5.1 Observations of pod-set and pod growth in normal and decapitated plants grown in a growth chamber.

Treatment	No. of flowering nodes	No. of nodes with pods	Total No. of pods	No. of pods per node	Fresh weight of pods (g) ¹⁾	Fresh weight per pod
Primus	28.9 ²⁾ +0.4	15.0 +1.2	20.1 +2.4	1.34	68.6 +8.7	3.42
Decapitated Primus without branches	14.3 ^{xxx} +0.4	8.8 ^{xxx} +0.8	21.9 +1.7	2.51	97.8 ^{xx} +6.0	4.46
Decapitated Primus with branches	14.2 ^{xxx} +0.3	6.5 ^{xxx} +0.6	15.4 +1.0	2.38	67.5 +5.0	4.39
Sv 0621 without branches	3.7 +0.2	3.2 +0.7	11.7 +1.8	3.69	52.9 +9.1	4.54
Sv 0621 with branches	3.6 +0.2	1.7 +1.1	4.7 ^x +2.1	2.80	21.5 ^x +8.8	4.60

x, xx, xxx: Significant differences at $P < 0.05$, 0.01 and 0.001 , respectively.

Decapitated tested against non-decapitated plants, Sv 0621 with branches tested against Sv 0621 without branches.

1) Fresh weight about 120 days after sowing

2) Means $\pm$ S.E.; $n = 20$

the number of pods per node still showed an increase, and pod weight was higher in both types of decapitated plants as compared with control plants.

Similar results were obtained for Sv 0621. However, Sv 0621 produced more laterals. The differences between plants with laterals and without were considerable.

Not only pod-set and lateral shoot development were affected by decapitation, but also the leaves, which soon after decapitation appeared more green, thick and leathery. Microscopic studies of leaves from plants decapitated four weeks earlier, revealed that anatomical changes had occurred. Table 5.2 shows decapitated leaves to be thicker as a result of increased size of the palisade parenchym layer and the spongy parenchym layer. Stomatal numbers were not affected but the size of the guard cells was increased.

Table 5.2 Leaf thickness, stomatal dimensions, and frequencies in leaves of intact and decapitated field bean plants grown in growth-chambers at 18°C and 150 Wm^{-2} . Measurements were performed on leaf number 17 four weeks after decapitation. (Control plants were not decapitated.)

Treatments	Control plants	Decapitated plants	Number of observations
Width of palisade layer (mm)	0.20	0.35	2
Width of spongy parenchym layer (mm)	0.20	0.35	2
Stomatal frequency (No. per mm^{-2})			
Upper epidermis	53 ± 1	55 ± 1	3
Lower epidermis	70 ± 2	70 ± 3	3
Length of guard cells (μm)	55.8 ± 1.0	59.3 ± 0.8	15
Width of guard cells (μm)	32.0 ± 1.3	33.5 ± 1.0	15

5.3.2 General and introductory measurements of photosynthesis

Figure 5.1 shows a typical light response curve for a fully expanded leaf of a field bean plant grown in the growth chamber. Leaves at this age showed a light saturation at an irradiance between $200\text{--}300\text{ Wm}^{-2}$. Thus, throughout the study an irradiance of 280 Wm^{-2} was chosen.

Figure 5.2 shows that P_N varied between the lower and upper leaves with a maximum about six nodes below the plant apex. Similar results have been reported in tobacco (Vaclavik 1975) and in field beans (Andreeva et al. 1972). The upper leaves have a lower P_N , since both r_s and $r_m + r_x$ are higher, but as the leaves develop both resistances decrease. The decline in P_N in older leaves is due mainly to increasing $r_m + r_x$.

5.3.3 Variations in leaf photosynthesis with age in normal and decapitated plants

Figure 5.3a shows variations in P_N with age for leaf 15 of control and decapitated plants and for leaf 8 of Sv 0621. In the figure the results from decapitated plants with laterals have not been expressed since they are similar to those of decapitated plants without laterals, although in general they were somewhat lower.

The very young leaf reached a maximum in P_N at an early stage. Thereafter P_N decreased with increasing age. However, the declining trend was temporarily changed into a second and a third maxima two and three weeks after the first maximum.

Decapitation totally changed this trend. Two days after decapitation P_N increased to a new maximum at $40\text{ mg dm}^{-2}\text{h}^{-1}$ after two weeks. Then there was a sudden decrease to a more normal $35\text{ mg dm}^{-2}\text{h}^{-1}$. However, after five weeks the leaf still assimilated more than $30\text{ mg dm}^{-2}\text{h}^{-1}$. Sv 0621 showed similar variations in P_N as in the decapitated plants.

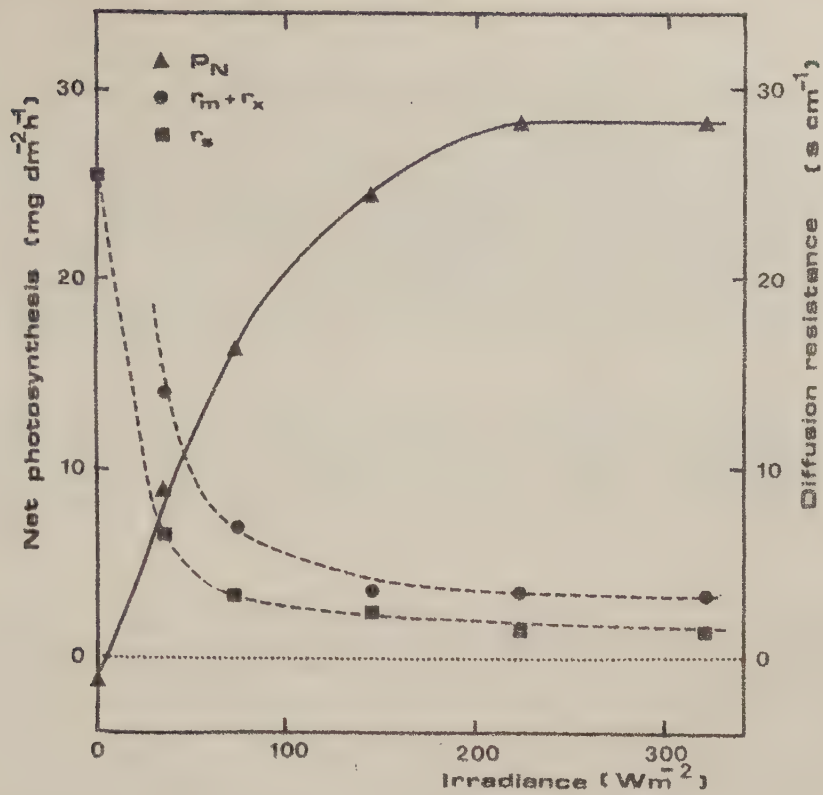


Fig. 5.1 Relationship between irradiance and net photosynthesis and diffusion resistances of a leaf consisting of the two outermost leaflets with an area of 17 cm^2 each (number 19 from base) on a plant of the variety *Primus* grown in a growth chamber with a daylight, at 18°C and an irradiance of 150 Wm^{-2} . Measurement condition: $328 \pm \text{CO}_2$, $20.9 \pm 0.1^\circ\text{C}$ leaf temperature, $r_a = 1.3 \text{ s.cm}^{-1}$, air pressure 762 mmHg .

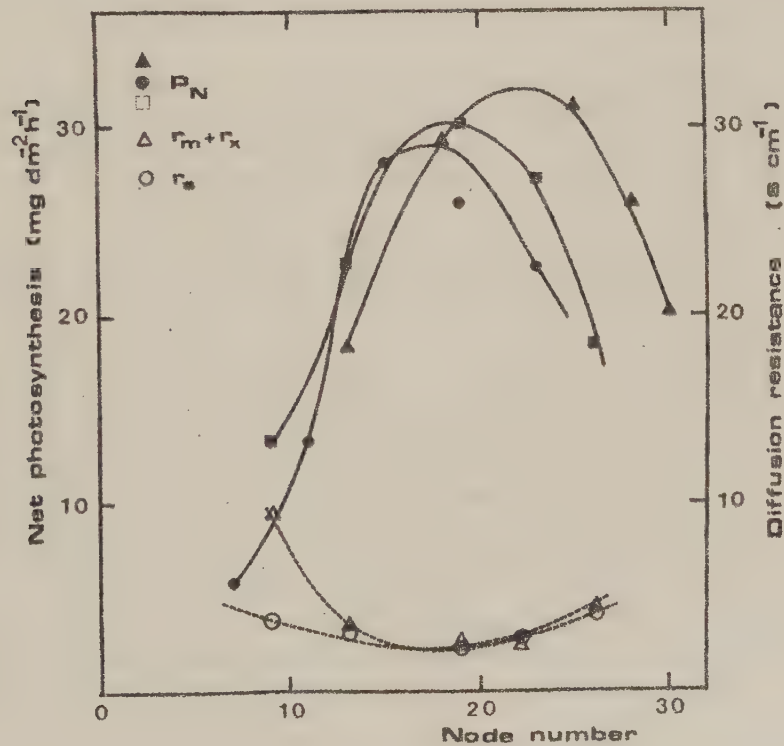


Fig. 5.2 Net photosynthesis and diffusion resistances of leaves of different nodes from three *Primus* plants with a varying number of nodes. Nodes were numbered from the shoot base. The plants were grown in a growth chamber at 18°C and 150 Wm^{-2} . ($r_m + r_x$) and r_s only shown for one of the plants. Measurement conditions: Irradiance 280 Wm^{-2} , 320 ppm CO_2 , $20.5 \pm 0.1^\circ\text{C}$ leaf temperature, 762 mmHg air pressure, and $r_a = 1.04\text{--}1.08 \text{ s.cm}^{-1}$.

5.3.4 Variations in diffusion resistances with treatment and age of the leaf

Variations in r_a were small since ventilation of the cuvette was constant, and leaf sizes only increased slightly after completed leaf expansion. Average r_a of control plants, decapitated plants, and Sv 0621 were 1.18, 1.27, and 1.31 s cm⁻¹, respectively. These are higher values than those reported in other studies, and implies that the ventilation of the cuvette could have been better in spite of the fan and a flow rate of 210 l · h⁻¹.

During the first four weeks r_s showed a constant value and then an increasing trend in control plants (Fig. 5.3c). In decapitated plants r_s showed a tendency to decrease after decapitation followed by a slightly increasing trend. In Sv 0621 r_s decreased throughout the experiment.

Variations in r_m+r_x in control and decapitated plants followed the same trend as r_s , but it was more pronounced and more coupled to variations in P_N (Fig. 5.3b). Within two days after decapitation a change in r_m+r_x occurred, although the main effect of decapitation occurred between the 4th and 7th day. Two weeks later r_m+r_x increased to a value similar to that just before decapitation. The main and steep increase of r_m+r_x in control plants occurred about four weeks after unfolding of the leaf.

5.3.5 Variations in specific leaf weight with treatment and age of the leaf

As the leaf developed specific leaf weight on a fresh weight basis (SLW_{fw}) increased slightly in control plants, whereas SLW_{fw} in decapitated plants and in Sv 0621 increased during the first three weeks after decapitation and then stabilized at a high value (Fig. 5.3e).

Specific leaf weight on a dry weight basis (SLW_{dwt}) decreased with age in control plants, whereas the trends for decapitated plants and Sv 0621 were almost the same as for SLW_{fw} (Fig. 5.3d). The sudden oscillations at the end of the experiment are difficult to explain.

5.3.6 Variations in soluble protein, RuBPCase, and chlorophyll contents with treatment and age of the leaf

The content of soluble protein declined with increasing age of the control leaves (Fig. 5.4a). However, the protein content was constant during the period when P_N reached its second and third maxima. Decapitation, on the other hand, resulted in an increasing trend after three days. When the protein content was calculated on a fresh weight basis the trend in control plants was unchanged, but in decapitated plants the protein content remained at a constant high level. The leaves of Sv 0621 followed a similar trend as those of decapitated plants, although the protein content was higher. Samples for determination of protein and chlorophyll were not collected from early stages in Sv 0621. The experiment was, however, repeated at a later date to determine protein and chlorophyll contents at earlier stages.

RuBPCase, the main fraction of soluble proteins, also declined with increasing age of the leaf (Table 5.3). Decapitation resulted in an increased synthesis or activation of the enzyme. The response to decapitation was fast but not fully accompanied by an increase of P_N (Table 5.3, and Fig. 5.6).

Chlorophyll variations were small in control plants until P_N started to decrease at the end of the experiment. In decapitated plants the chlorophyll content began to increase twelve days after decapitation, and then it increased throughout the study (Fig. 5.4b).

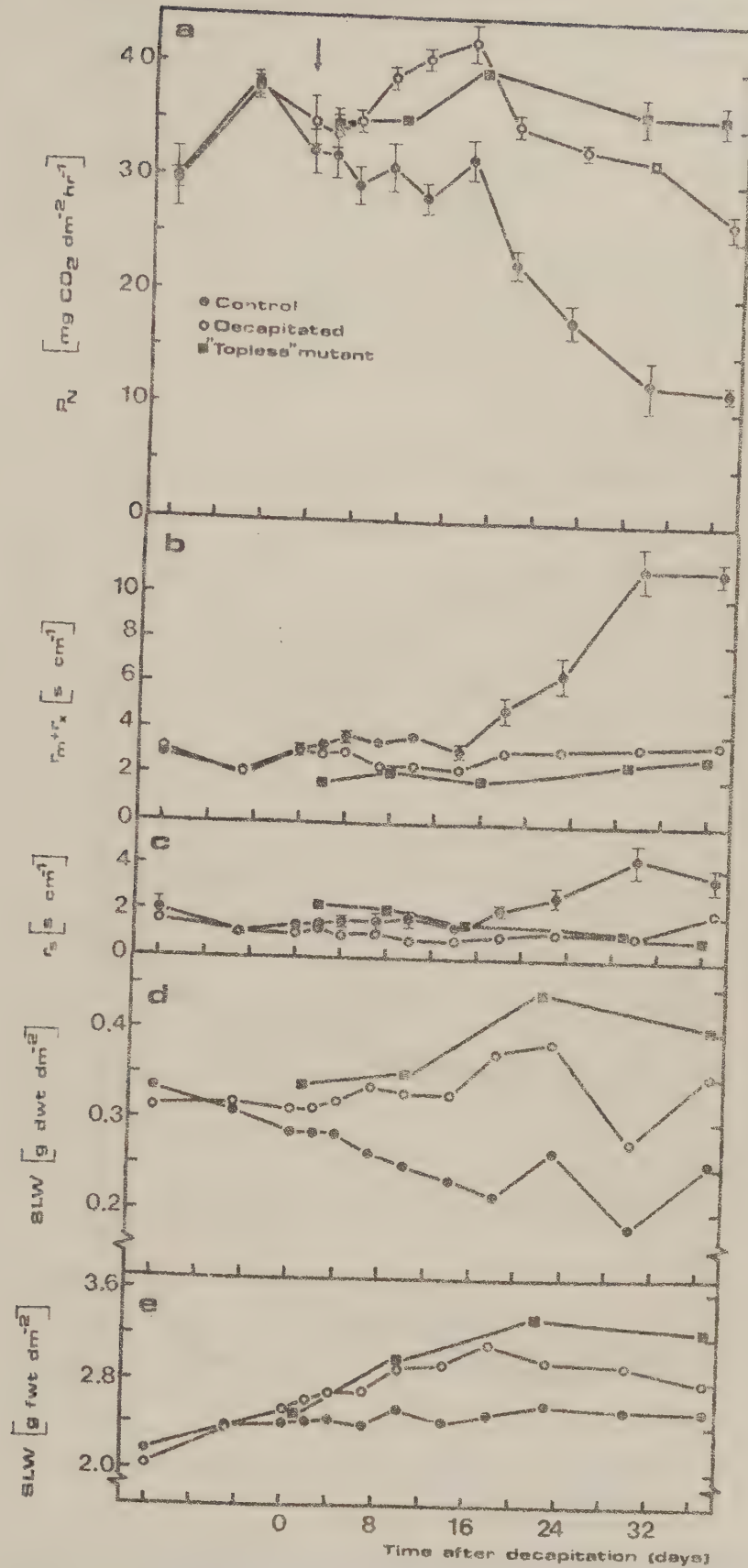


Fig. 5.3 Variations in photosynthesis (P_N), diffusion resistances (r_m+r_x) and r_s and specific leaf weight on a dry and fresh weight basis from unfolding of the leaves to maturity in normal and decapitated plants. Decapitation at day 0. Bars indicate S.E., $n = 3$. Where bars are missing S.E. is less than the size of the symbol.

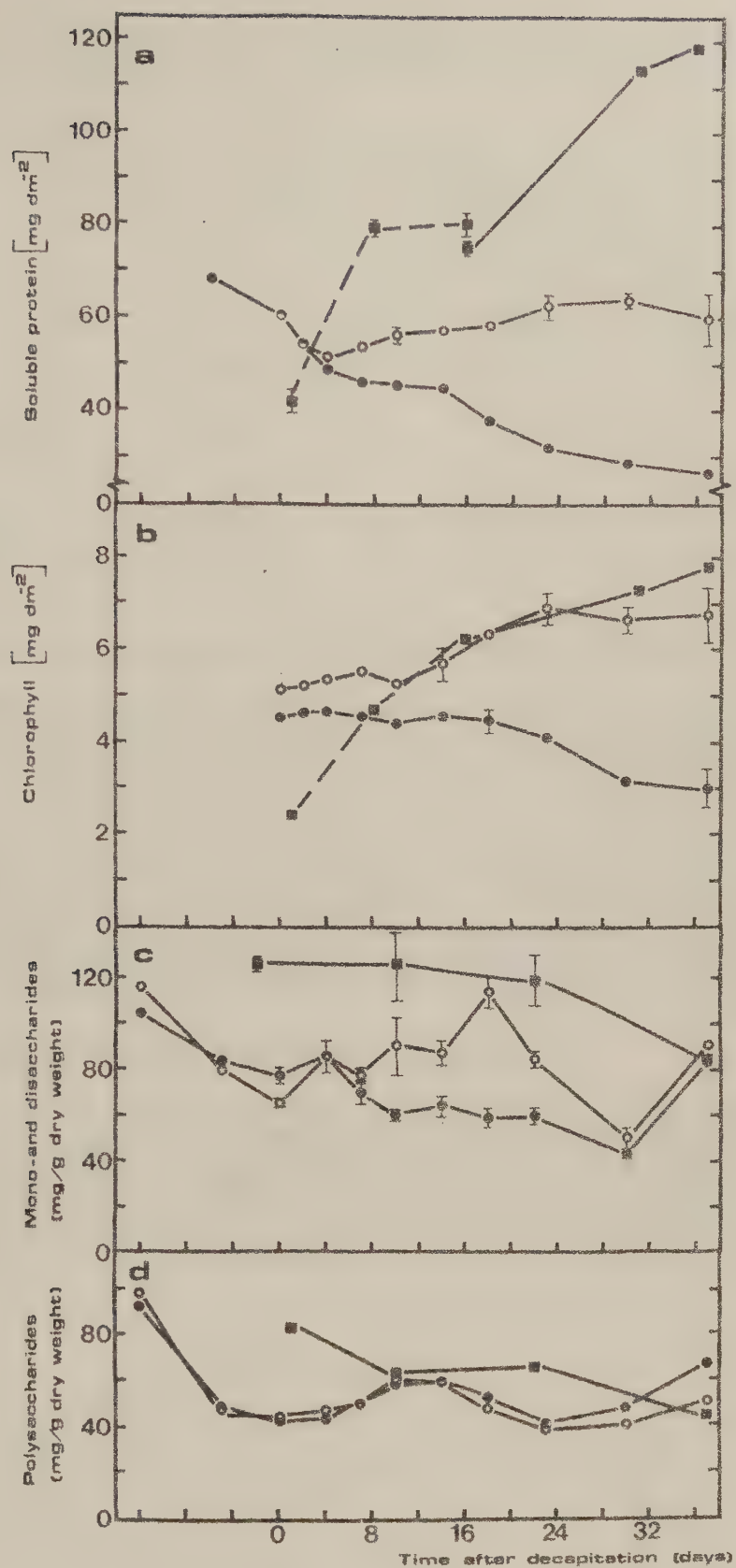


Fig. 5.4 Variations in soluble protein, chlorophyll and carbohydrates from unfolding of the leaves to maturity in normal and decapitated plants. Decapitation of day 0. Symbols the same as in Fig. 5.3

Table 5.3 Influence of decapitation of field beans on RuBPCase activity ($\text{cpm} \times 10^{-4} \text{ g}^{-1} \text{ min}^{-1}$) and net photosynthesis (P_N) ($\text{mg dm}^{-2} \text{ h}^{-1}$).

	Days after decapitation			
	4		24	
	RuBPCase	P_N	RuBPCase	P_N
Control	19.9 $\pm$ 0.9	29.3	16.1 $\pm$ 0.7	17.0
Decapitated without laterals	22.6 $\pm$ 0.6	34.8	21.1 $\pm$ 0.7	32.6
Decapitated with laterals	24.2 $\pm$ 1.1	35.8	20.7 $\pm$ 0.7	30.7

5.3.7 Variations in carbohydrates with treatment and age of the leaf

Carbohydrates in the leaf were separated into two fractions; those soluble in water and ethanol, mainly mono- and disaccharides, and those soluble in water and ethanol only after acid hydrolysis, mainly polysaccharides. The polysaccharide fraction was not changed by decapitation but did vary with age (Fig. 4d). It was high in very young leaves and declined as the leaf aged and as new leaves developed above. The variations in mono- and disaccharides were more in agreement with the variations in P_N . This is to be expected when the assimilation products are not transformed into polysaccharides or when the translocation rate out of the leaf is more or less constant.

5.3.8 Effects of decapitation on senescing leaves

P_N of leaf 18 on ten plants with a total of 28 nodes was measured and afterwards the plants were decapitated above node 19. P_N was then measured five times during the next 10 days (Fig. 5.5). After a lag phase of about 24 h P_N started to increase, as it had earlier in younger leaves. The main and steep increase occurred during the second and third day after decapitation.

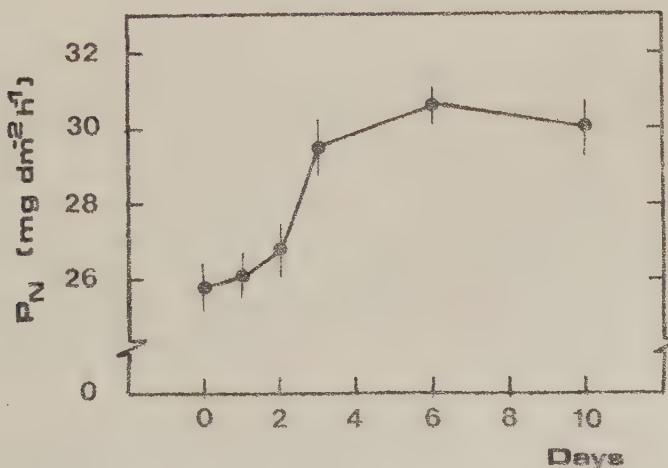


Fig. 5.5 Effects of decapitation on already senescing leaves. P_N measured on leaf 18. The uppermost 10 nodes removed at day 0. Bars indicate S.E. $n = 10$.

5.4 Discussion

5.4.1 Variations in normal leaves with age

In field beans, as in other crops studied, P_N varies with the ontogenetical status of the leaf (Fig. 5.3a, Ludlow and Wilson 1971, Gifford and Marshall 1973, Hodgkinson 1974, Fraser and Bidwell 1974, Woodward and Rawson 1976, and Hall and Brady 1977). Determinations of the rate of photosynthesis on leaves from the same plant but at different nodes have also shown similar patterns in field beans (Fig. 5.2), tropical legumes (Ludlow and Wilson 1971), lucern (Hodgkinson 1974), and tobacco (Václavík 1975).

The development of the leaf is characterized by an initial increase in P_N , as a result of a reduction in both r_s and r_m+r_x . Increase of stomatal and intercellular volumes (Meidner and Mansfield 1968) together with a developing photosynthetic apparatus affect r_s and r_m+r_x , respectively.

Maximum P_N is attained shortly before the leaf is full-grown whereafter P_N declines again. However, this declining trend is temporarily changed by events such as pod development. Similar fluctuations have also been reported in *Pisum* and *Phaseolus* (Flinn 1974, Turner and Bidwell 1965). However, in these studies depodded and debudded plants showed no such fluctuations.

The decrease in P_N with leaf age is associated with increased r_s as well as r_m+r_x , even if the magnitude of the changes is greater in r_m+r_x . There is as yet no full explanation for the increasing r_s with age. However, in other cells there is a continually changing pattern of enzyme and hormone activity (see Skene 1975), and this is probably also occurring in guard cells. A similar argument could also be valid as far as potassium ion concentrations in epidermal and guard cells are concerned (see Burrows and Milthorpe 1976).

With regard to r_m+r_x the strong correlation found between P_N and soluble proteins indicate that carboxylation reactions are limiting factors in the ageing leaf and that they affect r_x . In the present study the correlation coefficient between P_N and soluble proteins was found to be 0.95 both on an area and on a weight basis. This high correlation has also been reported by others (Wareing et al. 1968 and Andreeva et al. 1971). In decapitated plants, on the other hand, there was no correlation between P_N and soluble proteins. This is discussed further in 5.4.6.

The reduction of water soluble proteins is supposed to be the result of the degradation of mainly fraction 1 proteins in stroma. The fact that the capacity to produce new proteins diminishing with age (Woolhouse 1974), also plays a role. This is reflected in the structure of the chloroplast which changes from a well organized system of grana, thylakoids and dense stroma, to a chloroplast with a reduced grana system, where chlorophyll and fraction 1 protein concentrations are lower and where starch and lipid bodies occur in the stroma (Andreeva et al. 1972, Woolhouse and Batt 1976). Structural variations like these affected r_m as well as r_x .

Whether r_m or r_x both are affected first is uncertain. For example changes in plasmalemma or an accumulation of carbohydrates in the chloroplasts could affect diffusion of CO_2 and indirectly through lower photosynthesis, protein synthesis (Thorne 1973, Upmeyer and Koller 1973). However, the results from the carbohydrate analysis

do not support the idea of product inhibition (5.4.c, d). Therefore a direct effect on protein synthesis and thereby r_x appears to be more likely. For example in *Perilla* leaves there is a progressive loss of the capacity for protein synthesis, mainly because of the blockage of chloroplast ribosomal RNA synthesis. This is followed by a decreased synthesis of chloroplast ribosomes, which disturbs synthesis of fraction 1 protein (see Woolhouse 1974).

How these processes of sequential foliar senescence are initiated and regulated is relatively poorly understood. One theory supposes that the apex and other sinks divert the nutrients and growth substances away from the leaf. This could either be a sink effect because of the intensive cell division or maybe a direct hormone effect on the transport. Young leaves and meristems produce high amounts of auxins and gibberellins, and auxins are known to have an influence on the transport of metabolites in the phloem (Bowen and Wareing 1971, Patrick and Wareing 1973).

Auxins do not only affect the translocation of ions, nitrogen and carbohydrate substances but also the translocation of cytokinins (Morris and Winfield 1972). Therefore another theory has been proposed that centers around cytokinins and their effects on senescence. In a recent review on root cytokinins Skene (1975) summarizes the evidence for a cytokinin mediated control of leaf senescence. As the plant develops the supply of root cytokinins to lower leaves decreases, probably as a result of increased competition from upper leaves and from fruits and also because of a reduced cytokinin synthesis in the root (Sitton and Itai 1967). The reduction in cytokinin synthesis could either be a result of decreased root growth (Leonard 1962, Lawn and Brun 1974), or the result of a direct control by the shoot apex on cytokinin synthesis (Beever and Woolhouse 1974, Davies et al. 1977, Wareing et al. 1977).

5.4.2 The effects of decapitation

Decapitation effectively changed the normal processes of senescence in the leaf. Soon after decapitation P_N increased in both young and older leaves (Fig. 5.3a and Fig. 5.5) as a result of decreased r_s and r_m+r_x . The leaves became thicker, contained more soluble proteins, more chlorophylls, and more mono- and disaccharides. These are drastic changes and the question is why and how decapitation can affect the leaf in this way.

As discussed in chapter 4 decapitation reduces mutual shading of lower leaves. In this experiment, however, the leaves that were used for photosynthesis measurements from intact as well as from decapitated plants, were grown under similar light intensities, since precautions were undertaken to reduce the effect of mutual shading.

When a plant is decapitated mainly two parameters are changed. Firstly, a strong potential sink is removed and secondly, a source of hormones, mainly auxins and gibberellins, is also removed. If one draws parallels from studies of apical dominance (see review by Phillips 1975), auxins provided by the apical bud could serve as a correlation signal influencing synthesis and distribution of root cytokinin (Engelbrecht 1972). Cytokinin could thus be a trigger substance influencing leaf senescence (Woolley and Wareing 1972, Hodgkinson 1974, Woolhouse 1974, Beever and Woolhouse 1974, and Henson and Wheeler 1976).

In an experiment with decapitated pinto beans Pozsar (1978) obtained similar effects in photosynthesis and protein contents as observed in the present study. In addition he assayed cytokinin-like activity in the leaves and found an 8-fold increase in decapitated as compared to intact plants.

There is also indirect evidence that increased cytokinin activity after decapitation could be an essential factor in the leaves. Kinetin sprayed on leaves delays senescence and starts rejuventaion (Treharne et al. 1970, Dyer and Osborne 1971), increases RNA synthesis (Fletcher 1969), accelerates protein synthesis (Maass and Klämbt 1977), and promotes synthesis of chlorophyll as well as development of chloroplasts. Also other treatments that increase cytokinin activity in leaves such as the application of cytokinin to the roots (Thimann et al. 1974), and removal of buds and lateral branches (Meidner 1970, Gifford and Marshall 1973) have been shown to influence the leaves in a similar way.

The observed effects on the leaf after decapitation could thus be a result of increased cytokinin activity in the leaves. Cytokinins can be thought of as exerting their control on the stomata (Meidner and Mansfield 1968), and on the structure and activity of the chloroplasts. The extension of the parenchyma cells also increases the diffusion area of CO_2 and thus affects r_m (Nobel 1972).

5.4.3 The effects of branching

Normally *Primus* does not develop lateral branches. However, decapitation breaks apical dominance and relatively soon one or two lateral branches are developed. This probably affects the supply of nutrients and growth substances. Thus the effects of decapitation on P_N and other leaf characteristics are somewhat lower when branches are allowed to develop. Experiments with crops that normally develop lateral branches, such as *Lolium multiflorum* (L) and *Medicago sativa* (L), have shown that branching exerts a negative influence on P_N of the main shoot (Gifford and Marshall 1973, Hodgkinson 1974).

Branching has also been reported to reduce root growth in field bean (see Leonard 1962). The reduced growth could be the result of increased competition for nitrogen and carbon assimilates (Das Gupta 1972) and/or a result of increased mutual shading of lower leaves and since the latter mainly supply the roots with assimilates (Thaine et al. 1959) the roots starve. Experiments with different plant densities and light intensities have shown that competition for light is an important factor in regulating root/shoot growth. High densities and low light intensity favour shoot growth, whereas high light intensity reverses the effect (see review by Leonard 1962).

5.4.4 The effect of genetic determination of the shoot

The results of decapitated plants suggest that changes in leaf characteristics are caused by an increased supply of some elements that are normally translocated to or from the growing apex. Similar effects can be obtained by other treatments such as heat-girdling (see Phillips 1975), and treatment with triiodobenzoic acid (TIBA) (own unpublished results). This indicates that the wounding as such is not the cause. Therefore analogous results from determinate plants could be expected. With regard to decapitated plants, production of proteins, chlorophylls and the accumulation of carbohydrates resulted in very thick dark green leaves. However, relatively soon necrosis set in. Neither these nor the high contents of carbohydrates reduced P_N which remained high. Thus a feed-back inhibition mechanism could hardly be relevant in this case.

5.4.5 The effects of decapitation on respiration

In this study net photosynthesis and dark respiration, but not photorespiration, were measured. Seven days after decapitation of plants above leaf 18 (about ten leaves were cut off) dark respiration was increased from 0.93 ± 0.14 to $1.66 \pm 0.05 \text{ mg dm}^{-2}\text{h}^{-1}$. Comparable figures for P_N were 21.0 ± 0.8 and $32.5 \pm 0.7 \text{ mg dm}^{-2}\text{h}^{-1}$. That is, dark respiration increased relatively more than P_N .

More interesting than dark respiration is the respiration in light, i.e. photorespiration (Pr). Studies on lucerne have shown close correlations between P_N and Pr during the ontogeny of the leaf, and defoliation brought about an increase in both (Hodgkinson 1974). In *Phaseolus vulgaris* (L), Fraser and Bidwell (1974) found that true photosynthesis and Pr varied with age but without any positive correlation between them. Also in determinate lines of soybeans P_N and Pr showed a positive association with one another and the ratio of Pr and P_N was highly correlated with Pr indicating that loss of CO_2 became proportionately larger with respect to P_N as Pr increased (Bhagsari et al. 1977).

A positive correlation between P_N and Pr could be derived from their commonly shared glycollic acid and RuBP-carboxylase-oxygenase.

If these substances are decreased during ageing or increased after decapitation, both photosynthesis and photorespiration could be affected in a similar way. If, however, P_N is regulated rather by the diffusion of CO_2 than by RuBPCase activity, then the correlation is reduced.

5.4.6 Limiting factors for high rates of photosynthesis

This study shows that a plant normally does not use its entire photosynthetic capacity. Fig. 5.6 shows stomata and mesophyll conductances. Stomatal conductance is directly related to stomatal aperture and intercellular volume (Gaastra 1959). In normal untreated plants stomata and intercellular volumes do not have maximal aperture and size. After decapitation, however, they increase to a point where they no longer are limiting P_N . Now it is $r_m + r_x$ that is limiting. In certain other dicotyledons $r_m + r_x$ has also been found to be limiting at high rates of photosynthesis (Ludlow and Wilson 1971, Woodward and Rawson 1976).

The question that now arises is whether it is the diffusion and transfer of CO_2 from the sub-stomatal cavity to the chloroplast or the carboxylation and other dark reactions that are limiting P_N . When estimated as a residual resistance it is not possible to separate r_m and r_x . By estimating temperature dependence, however, it might be possible. As a diffusion resistance r_m is essentially temperature independent, whereas r_x is strongly dependent upon temperature (Gaastra 1959). However, in such studies gross photosynthesis in relation to temperature should be considered, and this is complicated by the presence of photorespiration (Jarvis 1971).

The close correlation found between in vitro activity of RuBPCase and in vivo P_N determinations (Björkman 1968 a, b, Wareing et al. 1968, Andreeva et al. 1971, and Wittenbach 1979) suggests that the carboxylation step is limiting photosynthesis. Therefore, the asymptotically decreasing curve for the in vitro analysed RuBPCase activity could be interpreted as r_x no longer was limiting P_N four days after decapitation (Fig. 5.6). However, it must be stressed that the RuBPCase assays were not made on the same plants as the P_N measurements.

5.4.7 Summary

In field beans as in most other studied dicotyledoneous plants there is a sequenceal senescence of the leaves. How this is regulated is not clear. By manipulating this process it has been shown that it is not a genetically directed or at least no irreversible change of the genome. Much of the results support the idea that it is a question of changing sink capacity to younger parts of the plant. Therefore, the answers could possibly be found in the mechanism of apical dominance and in the translocation of nutrients and hormones.

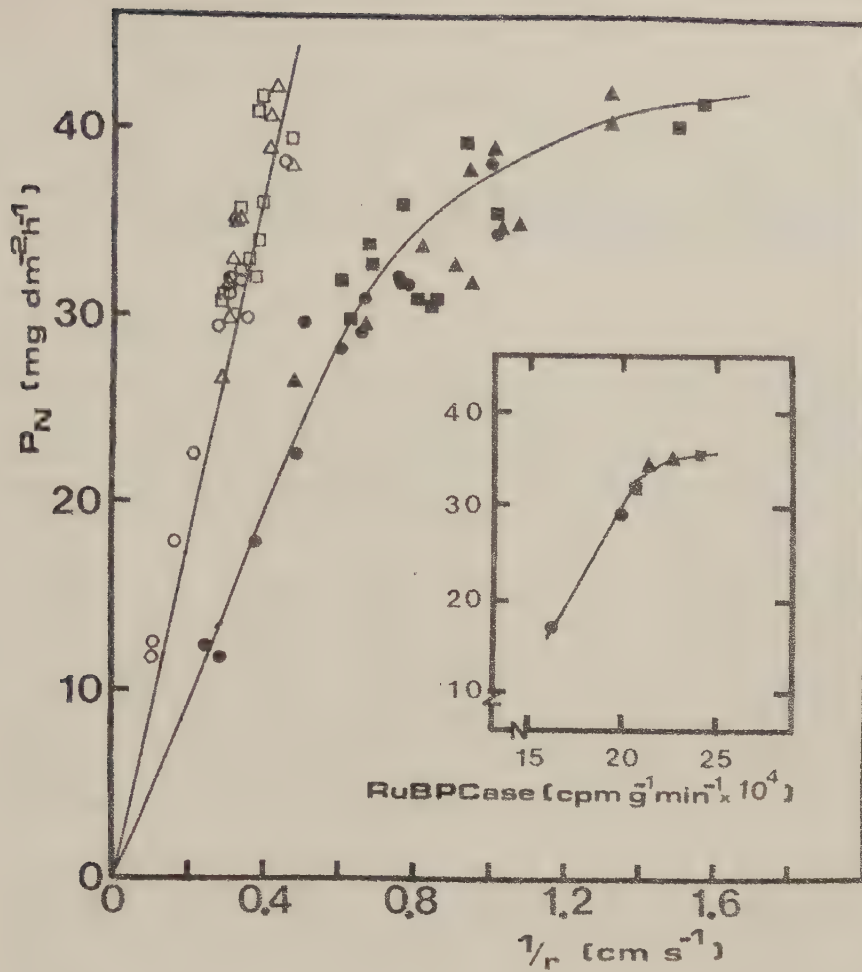


Fig. 5.6 Effects on stomatal conductances (filled symbols) mesophyll and carboxylating conductances (open symbols) and RuBPCase activity (small figure inserted) on P_N . ● control, ▲ decapitated without laterals and ■ decapitated with laterals.

Lack of nutrients and particularly growth-substances such as cytokinin in older leaves reduces protein synthesis and increases degradation of protein and chlorophyll which affects P_N . By removing strong sinks such as apical buds and other buds, this probably restores the sink capacity of older leaves. They became re-juvenated, i.e. they appear to function as young vital leaves and they sometimes are even superior to them. Protein and chlorophyll contents are increased, and neither r_s nor r_x seems to limit P_N . It seems rather that the diffusion of CO_2 in the mesophyll or/and chloroplast are limiting to a higher rate of P_N .

From the results it seems possible that a plant with determinate growth could compensate for a reduced leaf area with the aid of increased and extended CO_2 assimilation of older leaves. The results also support the idea that effects caused by decapitation are comparable to those in the mutant with determinate growth.

CHAPTER VI

INFLUENCE OF DECAPITATION ON PHOTOSYNTHESIS AND DIFFERENT YIELD CHARACTERS OF FIELD-GROWN FIELD BEANS

6.1 Introduction

So far the effects of decapitation of plants grown either in growth-chambers or outdoors in irrigated pots have been studied. Under these conditions vegetative growth is very extensive and since there is competition between vegetative and reproductive growth decapitation will have a very strong influence on the plant (see chapter 5).

In the field, however, environmental factors play a dominating role (El Nadi 1970, Sprent et al. 1977 a,b.). Soil moisture, in particular, has a dramatic effect upon vegetative and reproductive growth (Keatinge and Shaykewich 1977). Therefore, the effects of decapitation could to a large extent be affected by soil moisture. Another factor is the competition for nutrients and light. This is very difficult to study in the laboratory and therefore it is important to follow up the results obtained in the laboratory with field studies.

One of the aims of this study was to glean information about the effects of decapitation on yield. Experiments with decapitated field beans have been shown to have both positive and negative effects on yield. Kuznetsov and Bebin (1965) reported that defoliation 30-40 days before harvesting increased seed size and yield. Tamaki et al. (1972), however, reported a negative effect on both seed size and yield when the top zone was defoliated. However, since defoliation, instead of decapitation was employed there may have been some different responses. McEwen (1972), on the other hand, using decapitation got, although not significant, a decrease in yield of six per cent.

6.2 Materials and methods

6.2.1 Materials and treatments

1974:

Four commercial varieties, Primus, Sving, Skladia Kleine, Herz Freya and the mutant Sv 0621 were sown in a split-plot randomized block experiment with six replicates on May 21. The plots were 7 x 1.40 m and the seeds were machine drilled at a seed rate of 60 seeds per m². Before sowing the plots were fertilized with 32 and 60 kg per ha of P and K respectively. Weeds were controlled manually and insects were controlled with chemicals. When about nine inflorescences had developed the plants in every second block were decapitated with a pair of scissors. This was performed on July 25 on Sving, an early variety and on the others on July 30. In the middle of August there was a serious outbreak of the chocolate spot disease (*Botrytris fabae* Sard.) and particularly the leaf area of decapitated plants was reduced (including the mutant).

1975:

This year all varieties from 1974, but Sving, were used. Plots (10 x 1.40 m) were sown on April 21 in eight replicates without randomization.

Otherwise procedures were the same as those in 1974. Flowering started 60-62 days after sowing and finished 80-83 days after sowing. On July 18 when the production of new inflorescences had stopped, the plants in every second block were decapitated. Harvesting was carried out with a threshing machine about 115 days after sowing.

1976:

Five blocks with five plots (9 x 1.40 m) with Primus and one plot with Sv 0621 were sown late on April 16. Flowering started about 68 days after sowing and stopped 88 days after sowing. Decapitation of Primus was carried out at two stages. The first (on June 28) when eight to nine inflorescences had developed but no pod-set, and the second on July 6) when nine well developed inflorescences had developed and pod-set was visible at lower nodes. Decapitation and control plots were arranged in a split-plot randomized block experiment. As little as possible of the top zone was removed during decapitation.

The number of plants in each plot was counted on June 6 (3 x 0.7 m² counted in each plot), the number of flowers on June 28, immature pods on July 21 and mature pods at the end of August. Prior to harvesting 60 plants from each treatment were selected for a high number of pods. The pods were harvested node by node, dried and the seeds counted and weighed. The weights of the seeds were included with the weights of the machine threshed plants.

1977:

Two plots with Primus and six plots with Sv 0621 were sown in a split-plot randomized block experiment with four replicates on May 6. The plots were 10 x 1.4 m with a 14 cm row distance. Seed rate for Primus was 60 seeds per m² and for Sv 0621 it varied from 30 to 120 seeds/m². In Primus flowering started 51 days after sowing and at the end of flowering on July 30 half of the plants in the Primus plots were decapitated. At that time about 13-14 flowering nodes had developed. Subsamples were taken on July 23 to count the number of flowers and ovules in Primus and Sv 0621 (45 seeds/m² and 120 seeds/m²).

As in 1974 an outbreak of *Botrytis fabae* particularly reduced the leaf area of decapitated plants. This probably increased the maturation rate of Sv 0621 and decapitated Primus. They matured 142 and 150 days, respectively, after sowing whereas Primus matured 164 days after sowing. Prior to seed maturation subsamples were taken for analysis of yield components.

1978:

Seeds (Primus) were planted by hand (60 seeds m⁻²) in a bed with medium heavy soil and fertilized with 40 kg per ha of P and K. When necessary, the plants were watered in order to maintain a high soil moisture. At the tenth inflorescence stage half of the plants were decapitated (four subplots of each). The number of immature pods was counted 10 days after decapitation and at harvesting the number of mature pods, seeds per pod and seed weight were analysed. The plants were regularly sprayed with Benelate as a protection against *Botrytis fabae*.

6.2.2 Specific leaf weight

Specific leaf weight (SLW) was followed by leaf samples taken with a punch (12 mm $\emptyset$) and dried at 80°C for 48 h. All samples were taken between 10⁰⁰ and 11⁰⁰ on comparable leaflets of control and decapitated plants.

6.2.3 Photosynthesis

Photosynthesis was measured using a technique developed by Shimshi (1969). After exposing a small leaf segment (0.785 cm²) with ¹⁴CO₂ for 20 s (296 ppm CO₂ and a specific activity of 1.49×10^5 dpm $\cdot$ μ mol⁻¹) the segment was immediately punched out and placed in a scintillation vial containing 1 ml of 0.6 M solution of a surface active organic base in toluene (NCS, Nuclear Chicago) and allowed to solubilize overnight. The solution was bleached with 1 ml of a saturated solution of bensoylperoxide. 10 ml of a scintillation fluid (6 g $\cdot$ l⁻¹ PPO and 75 mg $\cdot$ l⁻¹ POPOP in toluene) was added to the vial and the sample was then counted in a Liquid Scintillation Spectrophotometer (Mark II, Nuclear Chicago).

6.2.4 Light measurements

Light measurements were carried out with a Kipp-Zonen Solarimeter (Delft, Holland), and a red filter (Schott Jena RG 8) was used to measure heat radiation. Photosynthetic active radiation, PhAR, was calculated by subtracting the heat radiation from the total.

6.2.5 Total leaf area per plant

Plants were collected from the plots and the leaves were measured node by node photoelectrically.

6.2.6 Statistical calculations

Standard error of the mean, SE, was calculated and differences between control and decapitated plants were tested for significance using the t-test.

6.3 Results

6.3.1 Variations in development of normal and decapitated plants during the period 1974 to 1979

Field beans are very much influenced by weather. Thus plant development in 1974 and 1977 was different from that in 1975 and 1976. The main reason for this was probably due to the fact that in 1974 and 1977 more rain fall and the weather conditions were cooler (Table 6.1)

The wet weather favoured vegetative growth and the plants appeared more like those in the growth chamber (see Chapter 5). The stems were thick, the leaves broad and a large number of inflorescences developed. In the dry summers, on the other hand, plant development was poor and flowers were produced only at 6-9 nodes.

Accordingly, decapitation had the greatest visible effect in 1974 and 1977. In 1974 decapitation at the time of flowering resulted in an increased pod-set particularly at the upper nodes, in contrast to normal plants (field observations), and leaf specific dry weights were

Table 6.1 Mean air temperature, rainfall and sunlight hours measured at Svalöv from 1973 to 1977.

		May	June	July	August	September
Mean air temperature 24 h (°C)	1973	11.4	16.4	18.3	16.7	12.6
	1974	11.0	14.7	15.1	16.4	13.5
	1975	11.6	15.1	18.4	20.2	14.9
	1976	11.3	15.1	18.1	17.5	12.2
	1977	11.8	16.0	16.1	15.5	11.7
Average from 57 years		10.9	14.6	16.6	15.9	12.5
Rainfall (mm)	1973	83	25	83	38	89
	1974	17	77	81	68	83
	1975	24	20	41	28	92
	1976	67	41	51	11	41
	1977	36	82	108	42	33
Average from 57 years		48	58	84	77	70
Sunlight (h)	1973	248	319	303	297	143
	1974	258	255	224	225	123
	1975	260	310	274	289	167
	1976	208	282	283	313	118
	1977	278	222	204	196	163
Average from 57 years		239	247	232	211	152

Source: SMHI Svalöv

also increased (Table 6.2). In 1977 decapitation was carried out one week after flowering. Thus the effects were not so obvious, although decapitated plants matured earlier.

In 1974 the outbreak of the chocolate spot disease, *Botrytis fabae*, seriously reduced the photosynthetic area of decapitated and mutant plants. The young upper leaves of non-decapitated plants were unaffected. Therefore, the decreased yield in decapitated plants in 1974 probably could be a result of too low a photosynthetic area (Table 6.3).

In 1975 and 1976 decapitation resulted in an increased leaf specific dry weight. The effect on seed yield was small with the exception of the early decapitation in 1976 that significantly reduced the average number of seeds per pod (Tables 6.3 and 6.4).

Table 6.2. Effects on specific leaf dry weight (SLW, g dm⁻²) after decapitation of field bean varieties grown in field in 1974. Leaf discs (0.98 cm²) were taken from leaf 15 on 40 plants of each variety between 10.00 and 11.00 a.m.

Variety	Days after decapitation									
	0		3		7		15			
	Control	Decapitated	Control	Decapitated	Control	Decapitated	Control	Decapitated	Control	Decapitated
Primus	0.356	-	0.329	0.407	0.319	0.483	0.385	0.560		
Skladia	0.337	-	0.371	0.392	0.410	0.547	0.411	0.534		
Sving	0.325	-	0.349	0.402	0.431	0.458	0.367	0.517		
Freya	0.351	-	0.381	0.391	0.382	0.480	0.352	0.525		
Sv 0621	-	0.395	-	0.426	-	0.490	-	0.517		
Mean ¹⁾	0.342	-	0.358	0.398 ^x	0.386	0.492 ^{xx}	0.379	0.534 ^{xxx}		
± s.e.	0.007	-	0.012	0.004	0.024	0.019	0.013	0.009		

x, xx, xxx: Treatment effects significant at P > 0.05, 0.01 and 0.001 respectively (mean ± s.e., n = 4)

1) Sv 0621 excluded

Table 6.3. Influence of decapitation on yield and yield components of field grown field beans in 1974 and 1975.

Year	Yield components	Primus		Skladia		Freya		Sving		Sv 0621
		Control	Decapi- tated	Control	Decapi- tated	Control	Decapi- tated	Control	Decapi- tated	
1974	Yield (kg/ha) ¹⁾	3014	2253 ^x	3126	2588	3061	2736	2990	2893	1308 ^{xxx}
	+S.E.	+132	+120	+201	+32	+220	+52	+140	+81	+143
	Weight per seed	0.377	0.353 ^x	0.433	0.401 ^x	0.358	0.344 ^x	0.332	0.308 ^x	0.348 ^{xxx}
	+S.E.	+0.001	+0.007	+0.006	+0.006	+0.003	+0.004	+0.002	+0.008	+0.002
1975	No. of seeds per plot	7833	6243 ^x	7094	6329	8386	7801	9018	9199	3687 ^{xx}
	+S.E.	+344	+234	+544	+138	+649	+211	+482	+226	+416
	Yield (kg/ha) ¹⁾	3149	3000	3152	3147	2400	2393	-	-	2260 ^{xx}
	+S.E.	+260	+163	+360	+110	+172	+41	-	-	+162

x, xx, xxx: Treatment effects significant at P < 0.05, 0.01 and 0.001 respectively; n = 3
Sv 0620 tested against Primus.

¹⁾ Seed yields corrected to 15% water content

Table 6.4. Influence of decapitation on yield and yield components of field grown field beans in 1976.

Yield components	Control	PRIMUS		1) Late decapitation	Sv 0621
		Early decapitation			
Number of plants per plot	536+39	568+26	546+14	677+39 ^x	
Yield (kg/ha) ^{2,3)}	2278+144	2175+149	2278+98	1619+199 ^x	
Yield per plant (g) ⁴⁾	5.30+0.31	4.75+0.26	5.28+0.28	2.88+0.76 ^{xxx}	
Number of pods per plant	5.55+0.40	5.50+0.36	5.71+0.23	4.17+0.18 ^x	
Seed weight per pod (g)	0.967+0.031	0.867+0.026 ^x	0.925+0.027	0.690+0.024 ^{xxx}	
Weight per seed (g)	0.409+0.004	0.413+0.003	0.414+0.002	0.369+0.004 ^{xxx}	
Number of seeds per pod	2.37+0.08	2.10+0.06 ^x	2.24+0.06	1.87+0.05 ^{xx}	

x, xx, xxx: Treatment effects significant at $P < 0.05$, 0.01, and 0.001 respectively.
Sv 0621 tested against Primus.

- 1) Early decapitation when eight to nine inflorescences had developed, late decapitation eight days later.
- 2) Seed yields corrected to 15% water content.
- 3) Number of pods per node was counted on 400 plants.
- 4) Calculated values using number of plants, number of pods per plant and weight per seed.

6.3.2 Distribution of pods and seeds in normal and decapitated plants

In *Primus* as well as in Sv 0621, flower-set was high at the first six flowering nodes in 1976. However, only half of the flowers set pods that remained until July 21, and some of these were also aborted at maturity (Table 6.5 and Fig. 6.1). Decapitation at flowering had a positive effect on pod-set but at maturity this was neutralized. Decapitation at the end of flowering, however, had no effect on pod-set.

Table 6.5 Flower and pod development in field grown field beans in 1976. Means of 15 plants selected for a high number of flowers and pods.

Material	Number of flowers at the lower six flowering nodes 29/6	Number of pods at the lower six pod bearing nodes 21/7	Total number of pods 21/7	Number of mature pods 30/8
<i>Primus</i>	36.6	16.4	19.1	12.9
Decapitated <i>Primus</i> (early) ¹⁾	-	19.5	23.1	12.4
Decapitated <i>Primus</i> (late) ¹⁾	-	16.4	19.0	13.1
Sv 0621	39.1	18.2	18.2	- ²⁾

1) See footnote 1, Table 6.4.

2) Destroyed

Figure 6.2 shows that the number of mature pods in the dry year of 1976 was highest at the second reproductive node and that the number of pods decreased rapidly up to the seventh node. Selection of plants with a high number of pods did not deviate from this trend. The effects of decapitation were also unaffected. In the wet year of 1977 the number of reproductive nodes was increased (Fig. 6.3). However, total number of pods per plant was not higher, as there were less pods on lower nodes. As in the early decapitation in 1976, decapitation one week after the end of flowering in 1977 resulted in a significantly altered distribution of pods. More pods remained at lower nodes but less at upper nodes relative to the control.

In 1976 in early decapitated plants the number of seeds per pod was lower than in late decapitated and control plants (Fig. 6.4 a). This is also true for pods at upper nodes in decapitated plants of 1977 (Fig. 6.5 a). In 1976 the decrease in seed size from the lower to the upper nodes was less than in 1977 (Figs. 6.4 b, 6.5 b). There were no significant effects of decapitation. However, both in 1976 and 1977 seeds at upper nodes were bigger in decapitated plants than in normal plants.

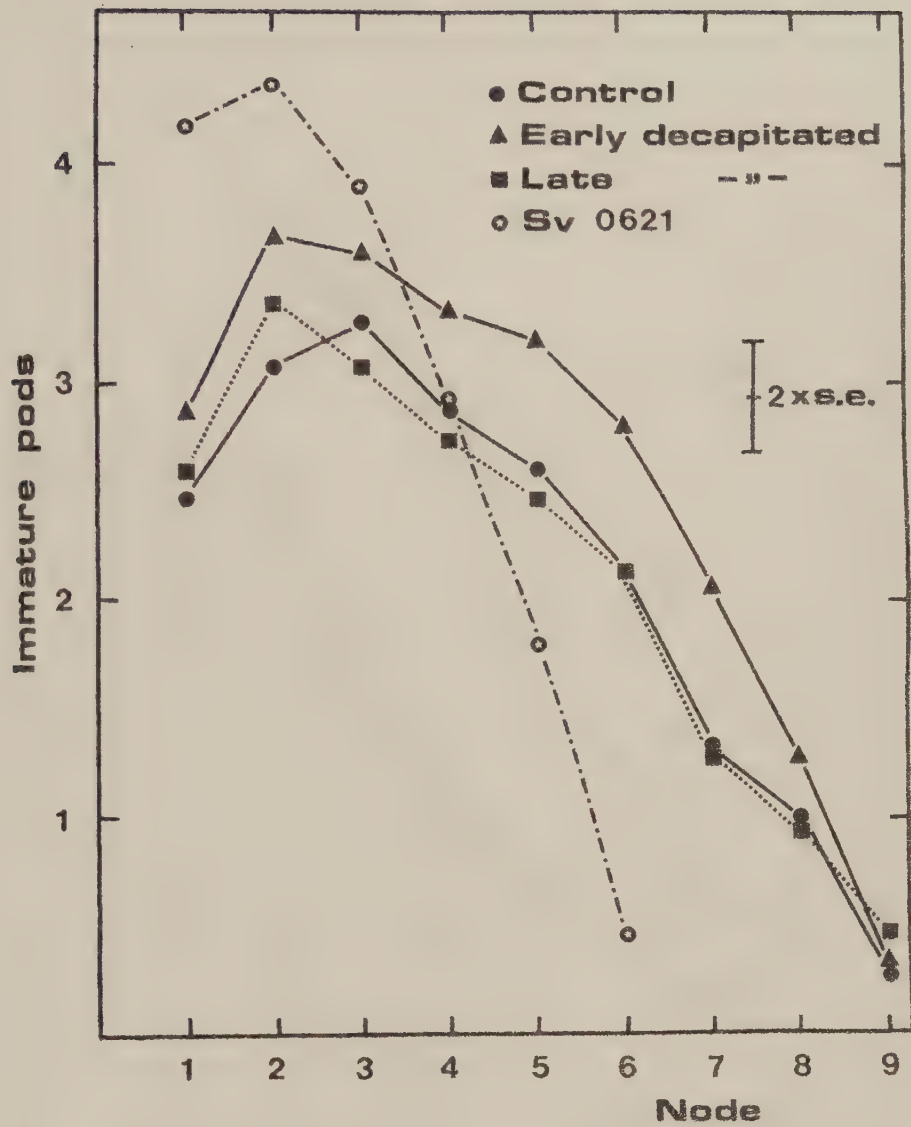


Fig. 6.1 Distribution of immature pods in normal and decapitated plants of *Primus* and Sv 0621 in 1976. Node 1 is the first reproductive node counted from the base. Early decapitation was carried out when eight to nine inflorescences had been produced and late decapitation eight days later. 20 plants from each treatment were analysed.

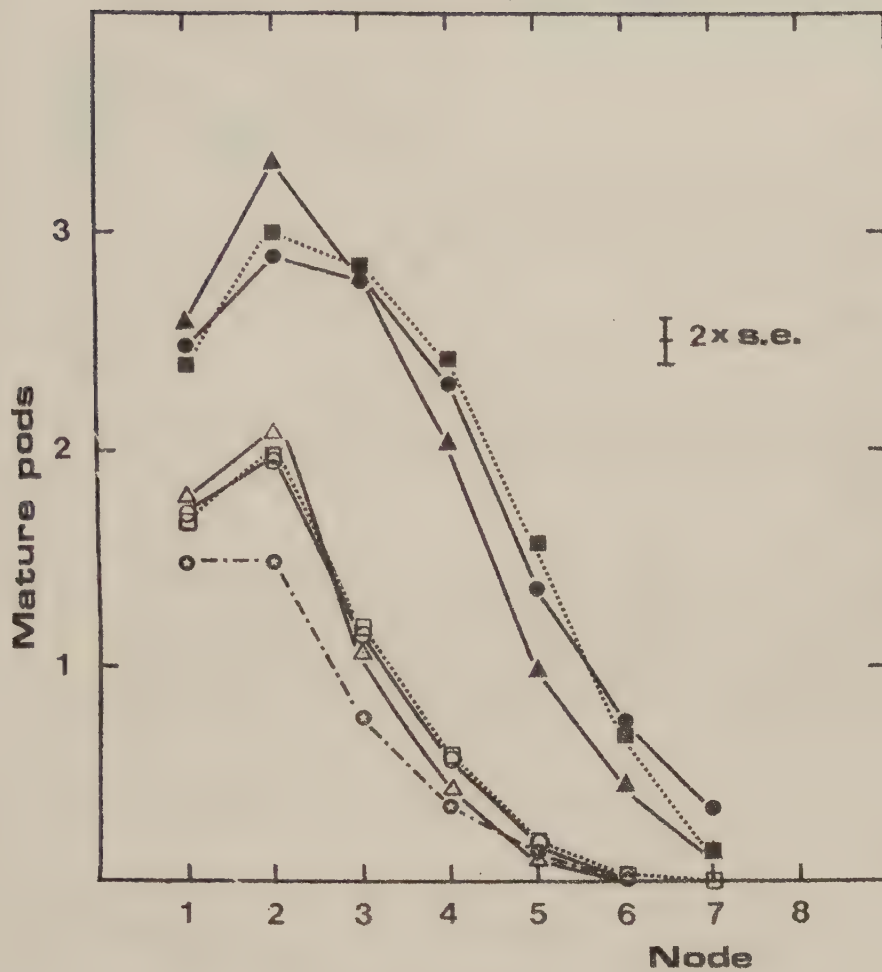


Fig. 6.2 Distribution of mature pods in normal and decapitated plants in 1976. The symbols are the same as in Fig.6.1 Closed symbols show the distribution of pods in 60 plants selected for high number of pods. Open symbols show the distribution of pods in 400 randomly selected plants.

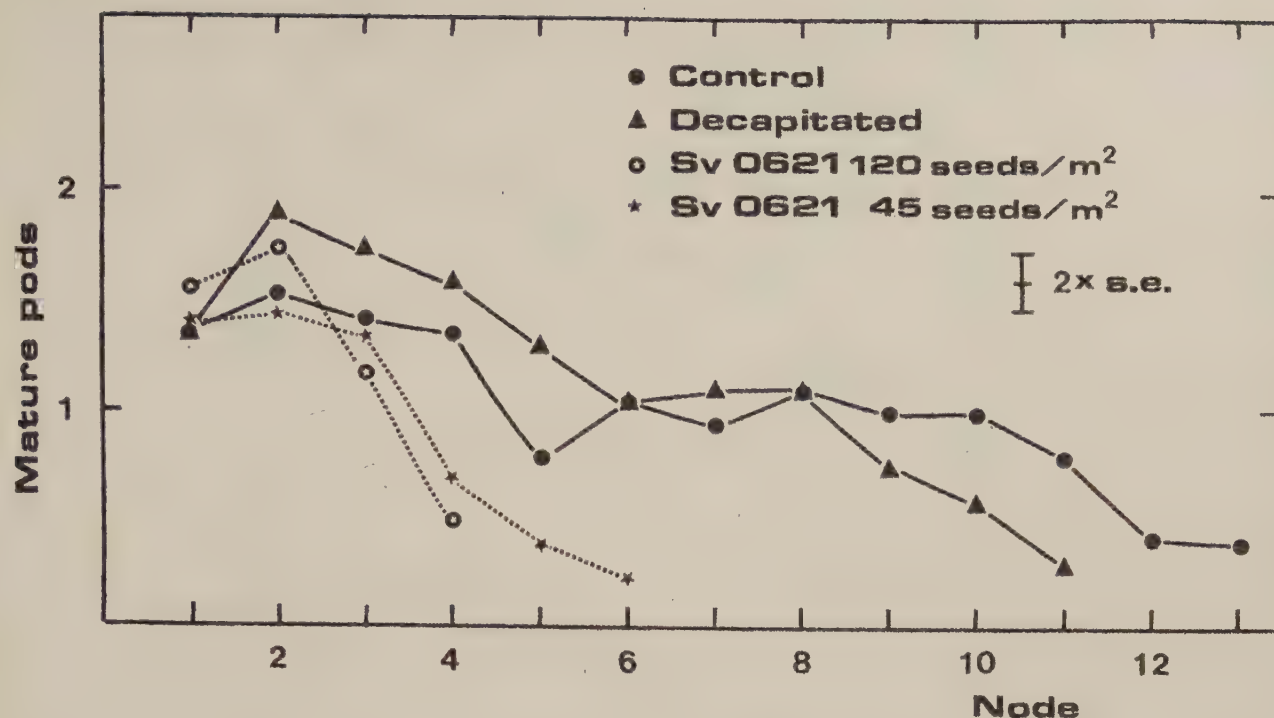


Fig. 6.3 Distribution of pods in normal and decapitated plants of *Primus* and Sv 0621 in 1977. Decapitation was carried out one week after the end of flowering. Node 1 is the first reproductive node counted from the base. 20 randomly selected plants were analysed.

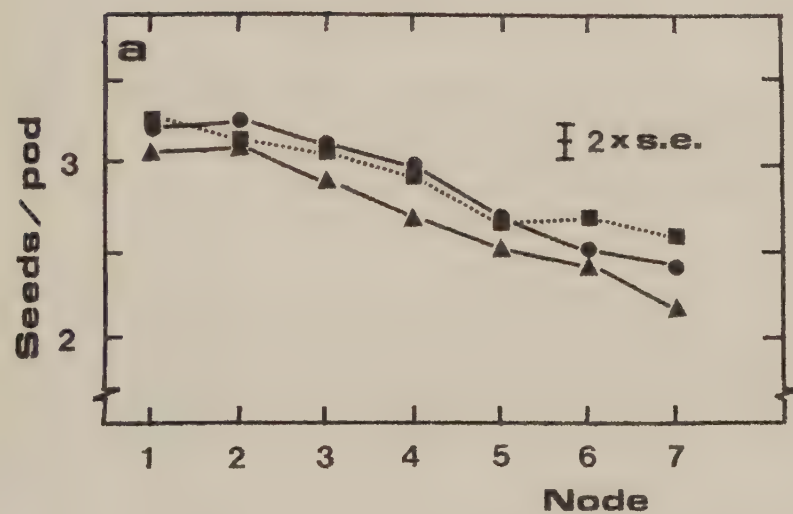
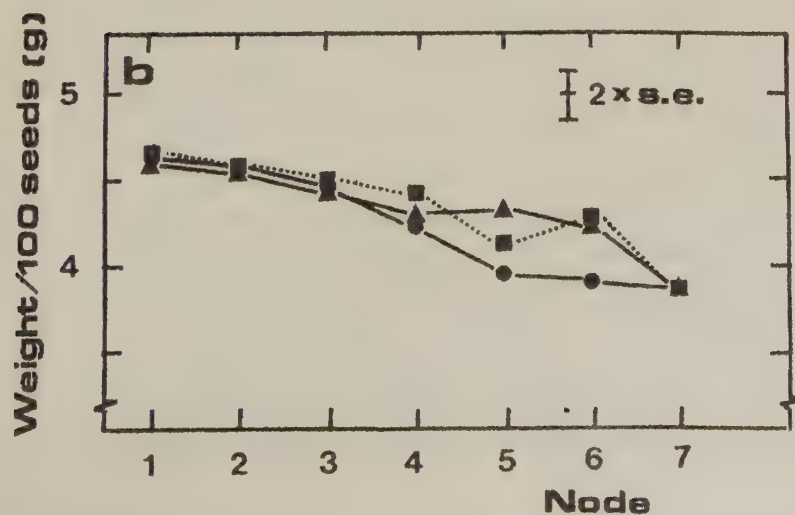


Fig. 6.4 a,b The influence of decapitation on number of seeds per pod and seed size in 60 selected plants in 1976.

Control ●
Early decapitated ▲
Late decapitated ■



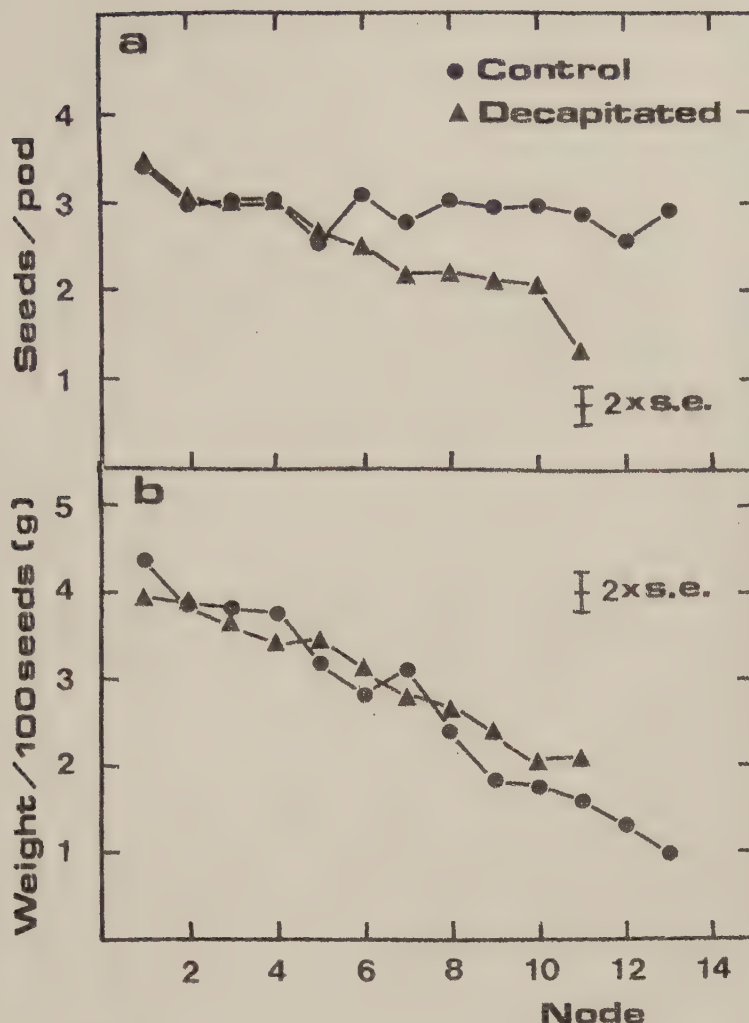


Fig. 6.5 a,b The influence of decapitation on the number of seeds per pod and seed size in 20 randomly selected plants in 1977. Symbols are the same as in Fig.6.3. Notice that the scale is different from Fig.6.4.

The difference in weather did not have any influence on pod distribution of the main shoot of Sv 0621. However, small differences were obtained in 1977 between densely and sparsely grown plants (Fig. 6.6). Both the number of seeds per pod and the seed size were decreased in the dense population as compared with that of the sparse population.

In Tables 6.4 and 6.6 the effects of decapitation on yield components for whole plants are summarized. In Table 6.4 the values are calculated from total seed yield per plot, the number of pods counted on 400 plants and seed size (weight). Table 6.6, on the other hand, is calculated from individually analysed and selected plants. Only the average number of seeds per pod was significantly influenced by early decapitation. In Sv 0621 all yield components were decreased as compared

with Primus. In 1977 the average number of seeds per pod was also decreased in decapitated normal plants (not significant) but the seed size was significantly increased and thus the yield was unaffected. In Sv 0621 the average number of seeds per pod as well as the seed size were lower in the dense population than in the sparse. In the dense population only 0.7 lateral branches were developed and these were responsible for about 19% of the total seed yield. In the sparse population 2.1 lateral branches were developed but their contribution to final seed yield was only 27%.

Table 6.6 Influence of decapitation and different seed rates on yield components in field grown field beans in 1977. Means of 20 plants selected for uniformity.

Yield component	Primus		Sv 0621	
	Control	Decapitated ¹⁾	120 seed/m ²	45 seeds/m ²
Weight of seeds per plant (excluding lateral branches) (g)	12.35±0.99	12.49±0.94	4.91±0.50	6.99±0.61 ^x
Weight of seeds per plant (including lateral branches) (g)	-	12.85±1.05	6.05±0.45	9.53±0.90 ^{xx}
Weight per seed (g)	0.312±0.015	0.355±0.008 ^x	0.346±0.023	0.388±0.013
Number of pods per main shoot	13.5±0.9	13.2±1.0	5.1±0.5	5.8±0.6
Number of seeds per main shoot	40.0±3.0	35.6±2.9	15.1±1.6	18.6±1.8
Number of seeds per pod	2.94±0.15	2.74±0.15	2.95±0.15	3.22±0.19
Number of lateral branches per plant	-	0.3±0.1	0.7±0.1	2.1±0.2 ^{xxx}

x, xx, xxx: Treatment effects significant at $P < 0.05$, 0.01 and 0.001 respectively.

Decapitated plants tested against undecapitated, 45 seeds/m² tested against 120 seeds/m².

1) Plants decapitated about one week after end of flowering.

2) The seeds were dried to constant weight at 80°C.

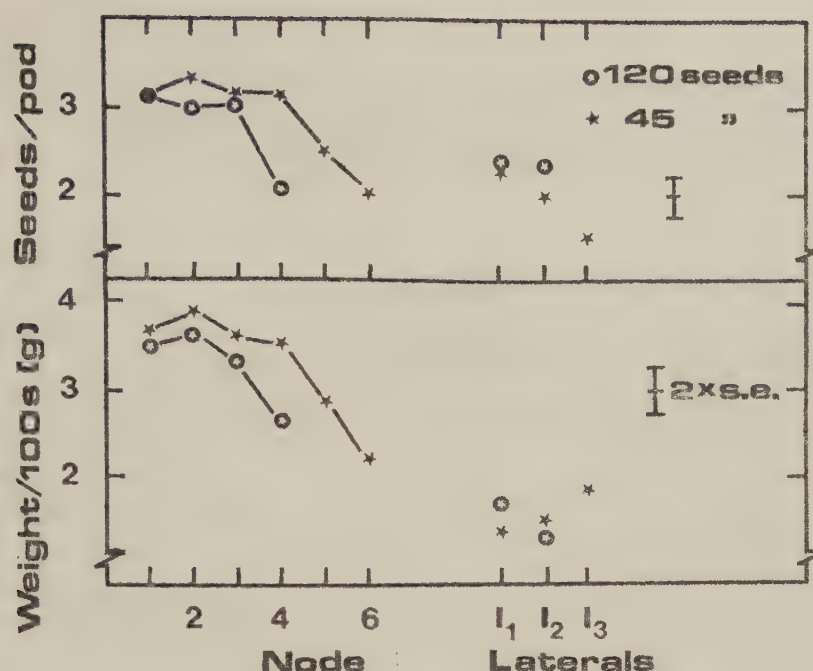


Fig. 6.6 a,b The influence of different seed rates on number of seeds per pod and seed size in 20 randomly selected plants of Sv 0621 in 1977. L₁, L₂ and L₃ denote lateral branches.

In order to ascertain whether there were any differences in the development of the ovules, 20 plants from Primus and Sv 0621 (120 seed $\cdot$ m⁻² and 45 seeds $\cdot$ m⁻²) were harvested at the time of flowering (Table 6.7). In some plants and particularly in Sv 0621, lower flowers were already fertilized and pod growth had started. Therefore, the figures in table 6.7 are averages of ovule numbers at different development stages. At this early date there were no differences in number of ovules. However, although not seen from the table, the number of ovules were less at lower nodes and more close to 4 at the upper nodes. This may indicate that some abortion had already occurred.

Table 6.7 shows that plants grown in a dense stand are taller but have shorter tap roots as compared with plants grown in a sparse stand. However, since the intact tap roots were not collected but only that part that remained after the plants had been pulled up, losses could vary. However, it was much easier to pull up the densely grown plants as obviously the roots were smaller and weaker. In this case lateral branch development did not seem to have any negative influence on the root growth (see Chapter 1). This discrepancy could, however, be explained. Every plant in the sparse population was well supplied with nutrients and the population was not closed. In the dense population the plants had to compete with each other for both nutrients and light. This probably reduced root growth more than the development of lateral branches did.

Table 6.7. Measurements of some morphological characters in field grown field beans in 1977. The plants were harvested during flowering stage. Means of 20 plants $\pm$ S.E.

Character	Primus	Sv 0621	
	60 seeds/m ²	120 seeds/m ²	45 seeds/m ²
Number of ovules per flower 1)	3.83 $\pm$ 0.09	3.82 $\pm$ 0.13	3.80 $\pm$ 0.08
Number of lateral branches from leaf axils	-	0.95 $\pm$ 0.25	1.50 $\pm$ 0.28
Number of lateral branches from stem base	-	0.70 $\pm$ 0.18	2.00 $\pm$ 0.29 ^{xxx}
Height of main shoot (cm)	70.4 $\pm$ 2.8	45.6 $\pm$ 2.2	39.3 $\pm$ 1.6 ^x
Length of tap root 2) (cm)	16.4 $\pm$ 0.6	11.5 $\pm$ 0.8	15.0 $\pm$ 0.7 ^{xx}

x, xx, xxx: Treatment effects significant at P < 0.05, 0.01 and 0.001 respectively.
45 seeds/m² tested against 120 seeds/m²

- 1) In some plants flowers of lower inflorescences were fertilized and small pods developed.
- 2) Refers to that part of the root that was recovered after pulling up the plants by hand.

6.3.3 Influence of decapitation on irrigated field beans

Irrigated plants showed an extensive growth similar to that in the growth-chamber or in the field during the wet season in 1974. In table 6.8 and Fig. 6.7 results of pod-set and pod abortion and yield as well as yield components are presented. The results are similar to those shown in 6.3.2. The main difference is reflected in a significantly decreased yield after decapitation. There was no increased lateral shoot development.

6.3.4 Field measurements of photosynthesis

Table 6.9 shows leaf photosynthesis (P) and photosynthetically active radiation (PhAR) at different leaf tiers in stands of normal and decapitated Primus. Although the canopy was thin in 1975 PhAR decreased rapidly from the apex to the base. Therefore, light was probably limiting P 3-4 nodes from the apex. Decapitation increased the light radiation that was penetrating down to lower leaves and P was increased to the same level as that of younger leaves of control plants that were exposed to similar light radiations.

Table 6.8 Influence of decapitation on yield and yield components of irrigated field beans in 1978.

Material	Number of immature pods	Number of mature pods	Number of seeds per pod	Weight per seed (mg)	Weight of seeds per plant (g)	Harvest index
Primus	21.2±1.2	11.4±0.7	3.13±0.03	379±5	13.5±1.0	0.50
Decapitated Primus ¹⁾	26.8±1.8 ^{xx}	9.1±0.5 ^x	2.96±0.10	371±10	9.9±0.7 ^x	0.50
No. of plants counted in each plot	8	8	25	25	25	

x, xx: Treatment effect significant at $P < 0.05$ and 0.01 , respectively.

1) : The plants were decapitated when ten inflorescences were developed.

Table 6.9

Photosynthetic active radiation (PhAR) and rate of photosynthesis (P) at different levels in field grown field beans (normal and decapitated plants of Primus) on July 28.

Weather conditions: bright sunlight, 28°C air temperature and low soil moisture.

Radiation figures represent means of 12 measurements + S.E. Rates of photosynthesis means of 6 measurements + S.E. Measurements were made between 9.30 and 11.30 a.m. and refer to leaves in the natural position and in undisturbed light environment.

Leaf number from stem base	Control				Decapitated ¹⁾			
	PhAR		P _N		PhAR		P _N	
	(Wm ⁻²)	Rel.	(mg dm ⁻² h ⁻¹)	Rel.	(Wm ⁻²)	Rel.	(mg dm ⁻² h ⁻¹)	Rel.
16-18	391±6	100	17.0±1.4	100	-	-	-	-
13-14	186±62	48	9.5±1.5	56	380±13	97	15.7±1.3	92
9-11	40±13	10	3.9±0.7	23	140±47	36	7.3±1.0	43
5-7	19±10	5	2.6±0.3	15	21±9	5	2.4±0.4	14

1) The plants were decapitated on July 18.

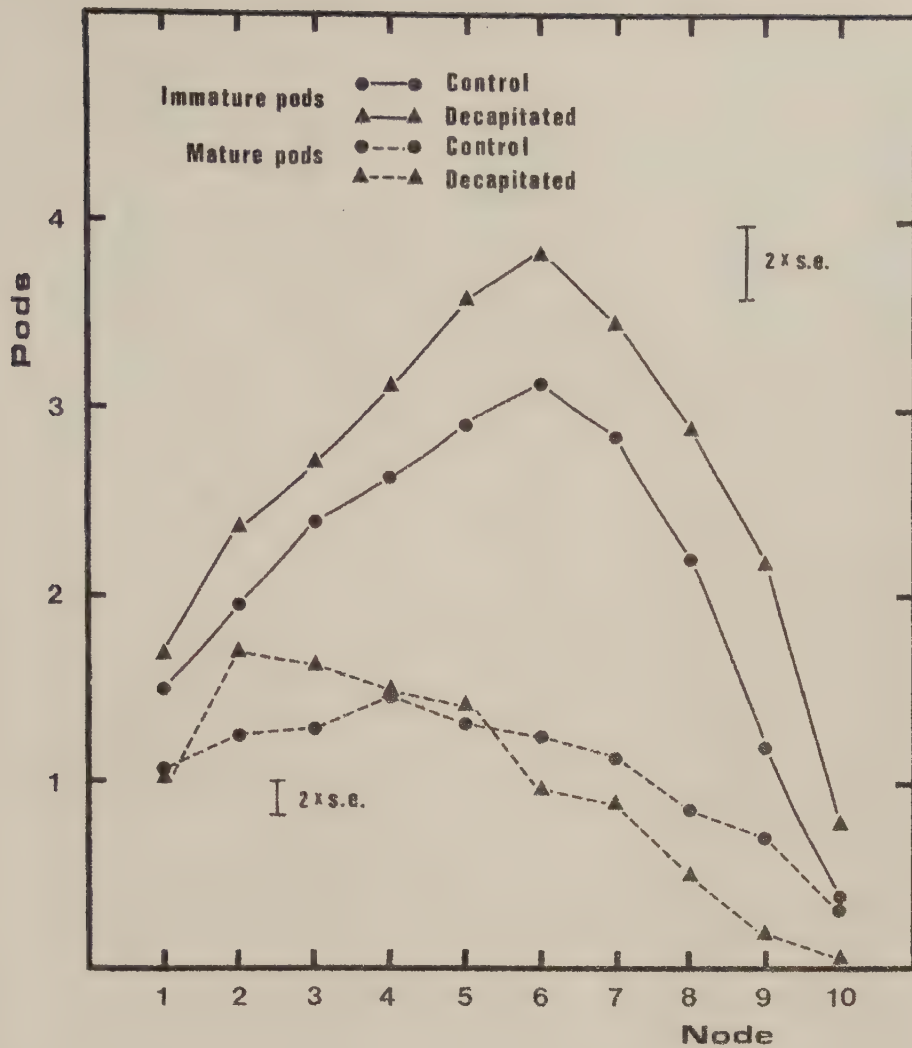


Fig. 6.7 The distribution of immature and mature pods in irrigated normal and decapitated plants of *Primus*. Node 1 is the first reproductive node counted from the base. Decapitation was carried out when ten inflorescences had been produced. 25 plants from each treatment were analysed.

In 1976 these measurements were repeated and extended (Table 6.10). As was earlier the case in the growth chamber, P varied with the age of the leaf i.e. P of leaf 13 decreased as the plant grew (see Fig. 5.3). Measurements of P at different tiers on the plant showed similar results as those in Fig. 5.2. Decapitation resulted in an increased P at leaf 13 and leaf 10. In cloudy weather P was decreased by 10-15% in the normal non-decapitated canopy, whereas it was decreased by more than 40% in decapitated plants. Decreased mutual shading was probably the main reason for the increased photosynthesis of leaf 13 and 10 in decapitated plants.

At the end of July leaf photosynthesis was measured at every second node on 13 plants in stands of control and decapitated *Primus* and Sv 0621 (Fig. 6.8). All measurements were done on leaflets in their natural position with undisturbed light environment between 10⁰⁰-12⁰⁰ during July 26-29. Measurements were also carried out on six plants

Table 6.10 Rates of photosynthesis (P_N), $\text{mg dm}^{-2}\text{h}^{-1}$) in field grown field beans in 1976
The measurements were made between 9.30 and 12.00 a.m. and refer to leaflets
in the natural position and undisturbed light environment. All values
represent means of 8 measurements $\pm$ S.E.

Date	Primus		Decapitated Primus ¹⁾		Sv 0621		
	leaf number 17-18	leaf number from stembase 13 10 6-7	leaf number 12	leaf number from stembase 10 6-7	leaf number from stembase 10 7-8	5-6	
2.7 ^{2,3)}	-	38.9 $\pm$ 2.9	-	-	37.8 $\pm$ 1.4	-	-
6.7	20.7 $\pm$ 2.7	24.0 $\pm$ 1.6	12.0 $\pm$ 2.2	6.1 $\pm$ 1.4	22.9 $\pm$ 2.2	16.1 $\pm$ 1.8	4.6 $\pm$ 0.7
20.7	18.4 $\pm$ 0.9	13.7 $\pm$ 1.4	7.7 $\pm$ 0.7	4)	15.0 $\pm$ 1.3	7.8 $\pm$ 0.7	4)
22.7	21.7 $\pm$ 2.7	15.3 $\pm$ 1.6	8.9 $\pm$ 1.0	4)	24.9 $\pm$ 2.7	14.7 $\pm$ 2.3	4)
%-decrease in cloudy weather ⁵⁾	15	10	13	40	47	32	6

1) The plants were decapitated above node 14 on June 28.

2) Weather conditions: Clear days (PhAR about 430 Wm^{-2}) July 2, July 6, and July 22.
Cloudy days (PhAR about 180 Wm^{-2}) July 20.
High soil moisture July 20, and 22. Medium high July 2, and low July 6.

3) Measurements made only at position B.

4) The leaves abscised.

5) Percentage decrease in P_N in cloudy weather (20.7) compared with P_N in bright sunlight (22.7).

on the outer perimeter of the plot. P showed an increasing trend from the lower to the upper leaves. In the control plants it was slightly curve-linear, but in decapitated plants and Sv 0621 it was almost linear and steeper. The result from non-decapitated plants from the outer perimeter followed surprisingly the same trend as that of control plants, meanwhile there was a positive effect on lower leaf photosynthesis in the decapitated edge plants from the outer perimeter. All measurements on the perimeter plants were carried out on leaves that were least shaded. Hence the results indicate that other factors than light radiation had a determining influence on P. However, these results are contradictory to those reported in Table 6.10. However, since water stress probably limited P here, the results may not be comparable.

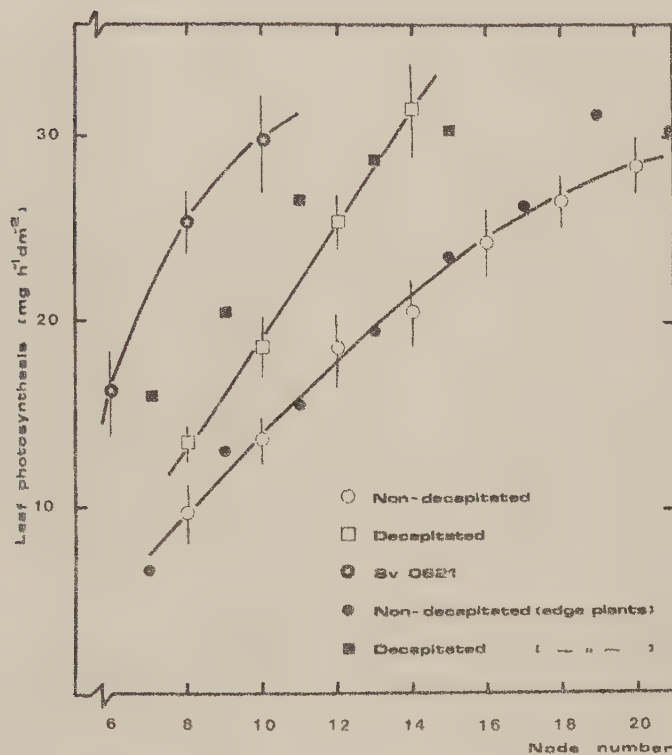


Fig. 6.8 Rate of photosynthesis measured on every second leaf of plants from populations of *Primus* and Sv 0621. Photosynthesis was measured with a Shimshi apparatus under natural light intensity between 10.00 and 12.00 on the 26, 27 and 29 of July. Nodes are counted from the base. Vertical bars indicate $2 \times S.E.$

Figure 6.8 together with leaf area measurements on 10 randomly selected plants were used to calculate total leaf photosynthesis per node and plant (Table 6.11). The vegetative top zone consisting of 34% of the total leaf area contributed 45% of the total leaf photosynthesis. After decapitation the rate of photosynthesis in the lower leaves was increased so that the reduction of total leaf photosynthesis was only 24%. In Sv 0621 the leaf area was 50% lower than that for *Primus* and leaf photosynthesis had decreased by 33%.

Table 6.11 Mean contribution to total plant photosynthesis by each leaf from 10.00-12.00, July 26-29. Leaf area was measured on 10 randomly selected plants of Primus and Sv 0621. Figure 6.7 was used to estimate the rate of photosynthesis. PhAR measurements were done with a Kipp&Zonen solarimeter at different levels in the stand.

Leaf number from stem-base	Primus			Decapitated Primus			Sv 0621		
	Leaf ¹⁾ area (cm ²)	PhAR (Wm ⁻²)	Total leaf photo-synthesis (mg h ⁻¹)	Leaf area (cm ²)	PhAR (Wm ⁻²)	Total leaf photo-synthesis (mg h ⁻¹)	Leaf area (cm ²)	PhAR (Wm ⁻²)	Total leaf photo-synthesis (mg h ⁻¹)
20	26.9	387	7.6	a					
19	38.2		10.5	a					
18	47.3		12.5	a					
17	50.3		12.7	a					
16	58.3	316	14.1	a					
15	62.1		14.2	a					
14	69.4		14.9	69.4 ²⁾	339	21.8			
13	72.2		14.4	72.2		20.5			
12	74.0	134	13.4	74.0		18.7			
11	90.0		14.8	90.0	216	20.0			
10	88.7		12.6	88.7		16.9	102.3	400	30.5
9	93.2	96	11.1	93.2	144	14.8	103.2	278	28.7
8	61.3		5.7	61.3		7.9	93.2		23.8
7	a ³⁾			a ³⁾			74.0	197	16.2
6	a ³⁾			a ³⁾			45.4		7.4
5	a ³⁾			a ³⁾			a ³⁾		
Total	831.9 +56.7		158.5	548.8		120.6	418.1 +22.4		106.6

1) Leaf area measurements on 10 randomly selected plants of Primus and Sv 0621.

2) No. of separate measurements of leaf area of decapitated plants.

3) a = absent, either because of abscission or decapitation.

6.4 Discussion

Seed yield in field beans is a function of three yield components: number of pods per plant, number of seeds per pod and seed size. The factor that determines their mutual effect on yield is the input of metabolites at varying times (Adams 1967, Thompson and Taylor 1977), but also different growth regulators seem to play an essential role (Addicott 1970, Bruinsma 1973). During the first phase of reproductive growth the number of pods per plant is fixed; then follows the number of seeds per pod and thereafter the varying input affects seed size. Accordingly, it is very important to have a high input during and immediately after flowering, otherwise too low a number of pods would be set. Even if an increased input at later stages would have positive effects on the number of seeds and seed size, there are limits as to how much these can increase. Therefore, the number of pods set has the greatest effect on yield (Ishag 1973 a, b).

Factors that determine the input of assimilates are the assimilation intensity of carbon and nitrogen and the quantity of these metabolites that are available for pod growth and vegetative growth. In 1975 and 1976 the weather was dry and the plants often suffered from water stress.

This lowered the assimilation rate and indirect vegetative growth. In 1974 and 1977 the weather conditions were wetter and this favoured vegetative growth and at the same time the increased competition lowered pod-set at lower nodes.

The effect of decapitation differed with the time at which decapitation was carried out. Early decapitation in 1974 resulted in high pod-set at upper nodes. In 1976 decapitation at the time of pod-set increased pod-set at all nodes and significantly changed the distribution of mature pods. However, when decapitation occurred seven days later there was no such effect.

An increased pod-set after decapitation could be a result of decreased competition for assimilates and growth regulators such as cytokinin (Engelbrecht 1972). Similar effects could also be expected if auxin proximal to the abscission zone is decreased (see Addicott 1970). Decapitation is known to reduce the amount of growth regulators transported basipetally (Phillips 1975).

Even if it is possible to increase pod-set by decapitation this is obviously not enough to give an increased yield. Instead, the excess pods were eliminated through abortion. Factors that might be regulating this abortion could be both nutritive and hormonal. In soybean, increased pod-set by temporary enrichment of CO₂ during flowering and early seed development also did not increase the yield. Photosynthesis has been suggested as the limiting factor (see Shibles et al. 1975). In this study photosynthesis of decapitated plants was not completely compensated for by an increased assimilation in lower leaves (Table 6.11). However, this does not necessarily mean that the supply of photosynthate was the primary factor determining the number of pods and seeds. The increased seed size as well as data obtained from earlier results (Chapter 5) in fact suggest the opposite to be true. Even if photosynthesis is not limiting at later stages, it could have been during earlier stages. Studies with *Phaseolus vulgaris* (L) have shown that the environmental conditions at pod-set were crucial in determining final yield, and that the rate of photosynthesis only at this stage was significantly correlated with yield (Peet et al. 1977).

In the dry years of 1975 and 1976 late decapitation had no effect on yield. However, since total yield was low even on non-decapitated plants, environmental factors may have played a dominate role. In 1977 the positive effects on pod-set were, as in early decapitated plants in 1976, negated by an increased pod and seed abortion, and yield was similar to that of non-decapitated plants.

In 1974 and in the irrigated plants of the experiment in 1978, yield was higher and decapitated plants yielded significantly less than non-decapitated. The results in 1974 and 1978 are in agreement with those reported by Gehriger (1978) and suggest that under high yield conditions decapitation influences yield negatively.

The results from plants grown in growth chambers or outdoors in pots suggest that there are mechanisms in the plant that regulate the assimilation of carbon. In the field these mechanisms probably are depressed by other factors and cannot function properly. Such factors could involve decreased drought resistance, nitrogen fixation and cytokinin production, all probably a result of reduced root growth after decapitation.

Because of the difference in soil moisture the different results obtained from Sv 0621 in 1976 and 1977 are to be expected. Apparently water stress in 1976 seriously affected both vegetative and reproductive growth. In 1977 the plants reacted similarly to those in the growth chamber, i.e. very extensive vegetative growth but poor pod-set. As opposed to 1976, the number of seeds per pod and seed size was not as low as in 1977. This indicates that the supply of assimilates was sufficient to fill the remaining pods.

The development of ovules is genetically determined and does not differ in *Primus* and Sv 0621 (Table 6.7). The lower number of mature seeds in Sv 0621 must then be the result of increased seed abortion. Factors that are known to influence seed abortion are water stress and lack of assimilates (see Shibles et al. 1975). Water stress can exert an influence both through hormones (see Addicott 1970) and through lower assimilation of carbon and nitrogen. Since the hormonal distribution pattern is changed in determinate plants it is possible that a stimulation in the production of abscission promoting hormones such as ABA and ethylene, as a result of water stress, could have a more negative influence in decapitated plants. In *Begonia* IAA produced by the flower buds keeps the pedicel tissue insensitive to ethylene and thus prevents abscission (Bruinsma 1976). To what extent a reduced supply of auxin from the apical bud could influence the interaction between auxin and ethylene in the flower is not known. El-Beltagy and Hall (1975), studying the endogenous levels of ethylene and auxin in field bean, showed that the ethylene level was well correlated with flower and pod abscission. In the dwarf type C182 flower abscission was very low as compared to normal varieties, and since the main flower production in C182 occurred before the level of ethylene had started to increase, they suggested that this was the reason for the decrease in flower abortion. However, the high level of auxin found at an early date in leaves and later in stems could also support the idea of an interaction between auxin and ethylene. It is also interesting that there were higher levels of auxin, abscisic acid and ethylene in the dwarf plants as compared to that in the normal variety inspite of much less vegetative growth. This could probably be explained by the increased lateral branch development of the dwarf type resulting in more growing points. If parallels are drawn from Sv 0621, the termination of the main shoot therefore may not be involved in reducing the total

plant hormone level, i.e. if there is development of lateral branches. In 1976 the growth of lateral branches was low but in 1977 it was high, and thus the results of particularly the seed abortion could support the hormone theory. However, since the abortion of an organ is the result of an interplay between several factors, where the influence of each factor is determined by others, field experiments could give very complex results.

Simulation computer models suggest that the availability of nitrogen limits yield in both soybeans (Sinclair and de Wit 1976) and cotton (Jones et al. 1974). Soybeans apparently need a large amount of nitrogen from vegetative tissues during seed-filling to sustain seed growth. If pod growth is increased by an increased rate of photosynthesis, and the rate of nitrogen absorption and fixation is unaffected, more nitrogen must be re-translocated from vegetative tissues and senescence of the plant is accelerated. One objection to this is that an increased photosynthesis is often followed by an increase in nitrogen fixation (Lawn and Brun 1974. Sprent and Bradford 1977). However, at the time of pod-filling, nitrogen fixation is low and an increased photosynthesis may not affect the nodule activity since the competition from pods is too strong. Accordingly, if the pool of re-distributed nitrogen is too low, the yield will be limited by the supply of nitrogen.

The soybean model has also been applied with reasonable success in *Vicia* sp. Thus similar effects could be expected also in field beans (see Sinclair and de Wit 1976). Therefore, the increased photosynthesis of the leaves and growth rate of the pods after decapitation could have negative effects on the yield as a result of limited supplies of nitrogen which influence the duration of the filling period.

Decapitation could also be responsible for reducing the nitrogen supply to the pods by causing an increased protein synthesis and retention of proteins in the leaves (see Chapter 5).

A third and direct way in which the nitrogen supply could be affected has been shown in a study by Hardy et al. (1971). They studied the differences in nitrogenase activity in soybeans with indeterminate and determinate growth habits. Their results showed that the nitrogenase activity was reduced at flowering but as the shoot apex in indeterminate plants continued to grow, the reduction was smaller than in determinate plants. This suggests that the upper growth, through hormonal or some other regulatory mechanism, could influence nodule activity.

From the above discussion the whole subject appears to be very complex and further investigations need to be conducted in order to throw more light on the role played by root growth, nitrogen fixation, hormone production, etc. Thus although it is possible to increase pod-set by decapitation of the plant, those plants in the field, as opposed to those in the growth chamber, seem unable to maintain the increased number of pods.

CHAPTER VII

GENERAL DISCUSSION AND CONCLUSIONS

7.1 Introduction

A shift from an indeterminate to a determinate growth habit is a radical process. The indeterminate plant has been favoured through natural selection (Stebbins 1974). However, the rather artificial cultivating conditions of today do not have much in common with the conditions during the time when the plants were subjected to natural selection pressures. Therefore, when a plant breeder selects plants he chooses those that give particularly high yield or in other ways satisfy him. However, by doing this many of the genes accumulated during evolution are lost and the plants do not then have the same adaptability to varying climatic conditions as the wild species. Since the field beans are already very sensitive to variations in the climate (Sprent et al. 1977), any change against the natural selection pressure would probably make the plant even more sensitive, and thus a change from indeterminate to determinate growth habit could have very serious consequences on yield and yield stability.

7.2 Possible advantages and disadvantages of an indeterminate and determinate growth habit

One reason why an indeterminate plant type has been favoured during evolutionary process probably lies in the fact that the flexibility of the plant to produce few or many flowers depends on the length of the favourable season (Stebbins 1974). This is illustrated in figure 6.2 and 6.3. In the dry season of 1976 flowers were only produced within about 15 days; while in the wet year of 1977 flower production occurred during 36 days. In 1976 more mature pods at lower nodes partly compensated for the lower number of flowering nodes. In 1977 a temporary water stress probably reduced the number of pods at node five, but as the conditions changed the number of pods at node 6-8 was not reduced as much as those at node five. From this it is obvious that determinate plants must be more sensitive to temporary periods of stress, since they lack the possibility to compensate for a low number of pods set by producing an increased number of pods at the upper nodes.

A continuous production of new leaves will also mean that the plant can rely on these new leaves for its supply of carbon assimilates. This is particularly important since the leaves quickly lose much of their capacity to fix carbon as they age (see Chapter 5). Furthermore the leaf area could be reduced by disease, insects and hailstorms. In this study the outbreak of *Botrytis fabae* occurred particularly on older leaves of normal and decapitated plants as well as on those of Sv 0621. However, in normal non-decapitated plants the upper leaves were not attacked, and thus the reduction of the productive leaf area was less. Griffiths and Amin (1977) have shown that lower leaves are most susceptible to infection and that the susceptibility decreases with increasing node number. However, decapitation, although making the leaves more juvenile again, seems to increase the susceptibility of both decapitated plants and Sv 0621.

A continuous growth of upper leaves after flowering, however, has a

negative influence on leaf senescence and pod-set. As new leaves are developed older ones gradually senesce. Pod-set is also lower in non-decapitated plants than in decapitated ones. This could either be a result of a reduced competition for nutrients or a changed hormonal balance.

A further complication concerns the apical dominance. The results reported in chapter 5 showed that it was necessary not only to decapitate, but also to control lateral branch development in order to have a maximum effect on leaf senescence and pod-set. Lateral branch development depends on how early decapitation occurs and on the weather (Gehriger 1978). Early decapitation and wet weather favour lateral branch development while decapitation after pod-set has less influence on the development of laterals.

Lateral branch development also has a negative influence on root growth (see Leonard 1962), while apical growth of the main stem is positively correlated with root growth (on a weight basis) (Gehriger 1978). If the apex, through a hormonal or some other mechanism, controls root growth, a determinate plant type could be negatively influenced. A decreased root growth will not only affect the water and nutrient status, but also production of cytokinins that presumably play an essential role in the plant (see review by Evans 1975).

An important factor to consider when evaluating the potential of a determinate plant type is to what degree photosynthesis limits yield. Field beans produce an excess of flowers and can with the right conditions supply a high number of pods with assimilates (Sprent et al. 1977). The limiting factor therefore seems not to be the storage capacity, but rather the supply of nutrients which is limited under field conditions. However, the sensitive mechanism that regulates pod and seed number must be taken into account. Temporary stress periods may reduce the number of pods and seeds resulting in the sinks becoming a limiting factor.

Keeping the indirect regulating mechanism of photosynthesis in mind, other factors such as nitrogen supply and hormone production have a more direct influence on the growth of field beans.

To sum up, a determinate growth habit (decapitated plants included) has a positive influence on pod-set. However, the determinate plant is more sensitive to environmental stress factors, and thus seed yield through pod and seed abortion will under some conditions be comparable with non-decapitated plants, but under other conditions be reduced.

7.3 Sv 0621 - and decapitated plants

So far decapitated plants have been compared with non-decapitated plants. The question that now arises is whether it is possible to transfer results obtained with decapitated plants to an improved "topless" mutant? In both the decapitated and the mutant plants stem growth is completed. In the mutant there is a gradual decrease in development of leaves and flowers, while in decapitated plants this is much more abrupt. A gradual decrease of apical growth gives the plant an opportunity to compensate for a decreased production of apical hormones. The incision, on the other hand, could influence turgor pressure, hormone production and air circulation in the stem cavity.

In spite of the above listed differences, plant development, C^{14} -distribution patterns and the effects on different leaf characteristics were similar. Thus an improved "topless" mutant could be expected to react in the same way as a decapitated plant.

7.4 Breeding suggestions for an improved plant type in field beans

The above discussion seems to eliminate the determinate plant type as an ideotype for field beans. However, since the negative effects on yield were small and were influenced by the stage at which decapitation was carried out, it is possible that a determinate plant could yield as much as an indeterminate one, if the termination of apical growth is late enough. However, it seems more practicable to look for intermediate types similar to those found in soybeans (Chapter 1).

Keeping the strong competition between vegetative and reproductive growth in mind, it is also essential to look for a plant type that flowers late and uniformly and set pods during a period of low vegetative growth. This is favourable to root growth and increases the re-translocatable pool of nitrogen and carbon assimilates that could have a determining influence upon pod-set and abortion.

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